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E. TREWAVAS

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BY

ETHELWYNN TREWAVAS

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TRUSTEES OF
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I ON THE CICHLID FISHES OF THE GENUS *PELMATOCHROMIS* WITH PROPOSAL OF A NEW GENUS FOR *P. CONGICUS;* ON THE RELATIONSHIP BETWEEN *PELMATOCHROMIS* AND *TILAPIA* AND THE RECOGNITION OF *SAROTHERODON* AS A DISTINCT GENUS

By ETHELWYNN TREWAVAS

ABSTRACT

Pelmatochromis nigrofasciatus Pellegrin is not, as has been suggested, a synonym of *P. ocellifer* Boulenger. The two species are defined and their relationships are discussed. The name *Pelmatochromis exsul* Trewavas was based on a misidentification of young *Hemichromis bimaculatus* Gill. Recognition of this fact removes the only record of *Pelmatochromis* from East Africa. A new genus is proposed for *P. congicus* Boulenger and a key to the species of *Pelmatochromis* is given. Reasons are given for excluding *Pelmatochromis* from *Tilapia* and retaining *T. busumana* in *Tilapia*. *Sarotherodon* Rüppell is considered to require full generic rank and *Tilapia* and *Sarotherodon* are defined.

Pelmatochromis Steindachner, 1895, type species *P. buettikoferi* Steindachner, by subsequent designation by Regan (1922), was restricted by Thys van den Audenaerde (1968a) to the species without a boot-shaped pad on the roof of the pharynx and with microbranchiospines on the outer sides of the second, third and fourth gill-arches, a restriction with which I agree.

Later, Thys (1968b) included *Pelmatochromis* in *Tilapia* and put *Tilapia busumana* (Günther, 1902) in the same subgenus. I dissent from both these opinions, and the present exercise arose from my examination in this context of *P. ocellifer* Boulenger, which Thys stated to have bicuspid teeth in the young. This, with the presence of a tilapia-mark on the dorsal fin in the same species, was his reason for including *Pelmatochromis* in *Tilapia*.

Dr M. Poll and Dr Thys kindly lent me some of the young '*P. ocellifer*' that had the bicuspid teeth and when, on comparing them with the only slightly bigger holotype of *P. ocellifer*, I told them that I thought they were not that species Dr Poll very kindly lent me a collection of specimens from the Museum at Tervuren that had been determined as *P. ocellifer*. They included two true *P. ocellifer* and 81 of the other species, which, as I now hope to show, is *P. nigrofasciatus* (Pellegrin), the types of which I examined in Paris some years ago, thanks to the kindness of the late Prof. Bertin.

With the holotype of *P. ocellifer* and the specimen figured by Boulenger (1915) we now have at Tervuren and BM(NH) four specimens of that species, respectively 63, 64·5, 85 and 100 mm in SL. In comparing characters showing allometry I use only specimens of the other species within this size-range, but for meristic characters I include also smaller and bigger fishes, up to SL 137 mm.

The two species have in common the following characters:

Scales 27–28 in the lateral line series, 14–16 around caudal peduncle; pattern of circuli in some scales roman, in others gothic (see p. 14 and fig. 10). Caudal peduncle very short, its length 0·5–0·8 of its depth. Depth of body 41·5–47·5% SL, length of head 35–39. Pectoral fin pointed or rounded, but not falcate, apparently complete in only two of the *P. ocellifer*, in which its length is 32·3–35·0% SL; in the other species it is 27·3–32·3%, shorter than head. Dorsal formula XIII 11–12, XIV 10–12 or XV 10–11, modal formula in *P. nigrofasciatus* XIV 11, modal total 26; a different formula in each of the four *P. ocellifer* (XIII 11, XIV 10–11, XV 11). Dorsal and anal soft rays produced in adult so that when they are laid back they reach a vertical in the posterior 2/3 of the caudal; pelvic ending in a long black filament extending to some part of the anal fin, in some as far as the hind end of its base; these prolongations occurring in both sexes. Caudal bluntly rounded, or truncate in the middle and rounded at the corners.

Except in interorbital width and length of premaxillary pedicels, proportions of parts of head alike in both species:- length of snout 29–36% length of head; diameter of eye 23–29; depth of preorbital 16·0–22·5, always smaller than eye; length of lower jaw 35–39.

Microbranchiospines present on outer sides of 2nd, 3rd, and 4th arches.

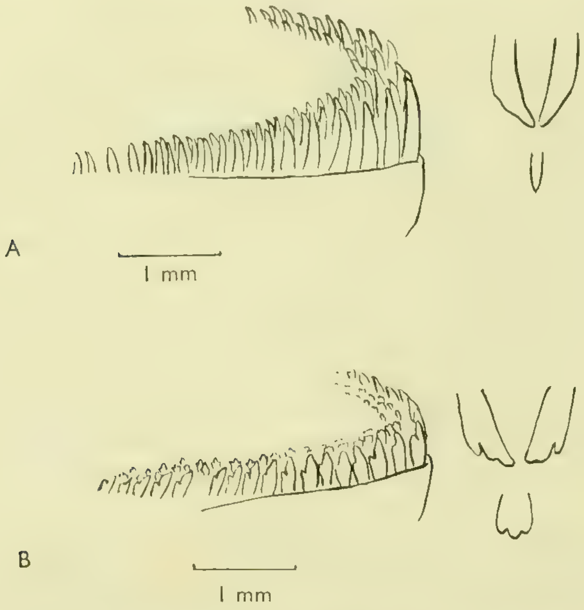


FIG. 1. A. Teeth of lower jaw in the holotype of *Pelmatochromis ocellifer*, SL 64 mm, and two outer and one inner teeth a little more enlarged. B. The same of *Tilapia ruweti* of SL 71 mm.

An intense opercular spot; a tilapia-mark on base of dorsal at junction of spinous and soft parts.

The distinguishing characters and synonymies are as follows.

P. ocellifer

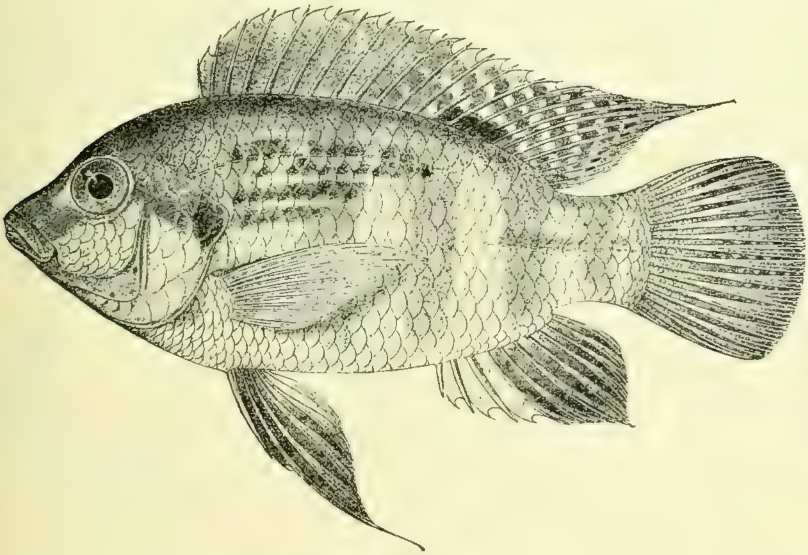
Boulenger, 1899 : 104; id. 1901 : 421; id. 1915 : 391 fig. 264.
Paratilapia nigrofasciata (nec Pellegrin); Steindachner, 1914 : 54 (R. Ja).

HOLOTYPE. BM(NH) 1898.7.9.16, 64·5 mm in SL, from Monsembe (Mosembe), Middle Congo, ca. 1°20′ N, 19° E. coll. J. E. Weeks.

Teeth unicuspid, curved cones at all known stages, in bands 3–5 teeth wide in both jaws, 38–52 in outer series of upper jaw, about 6 anterior outer slightly longer than the rest, inner a little shorter than the outer (fig. 1A).

Premaxillary pedicels 27·7–30·1% length of head; interorbital width 30·1–33·2%.

Gill-rakers on first arch (2–3) + 1 + (6–7) (fig. 2). Pad on roof of pharynx not boot-shaped, no groove or a very shallow one before it. Width of lower pharyngeal bone 24·0–29·5% length of head; teeth of its middle rows few and spaced, some blunted (fig. 4).



Pelmatochromis ocellifer.
Monsembe.

FIG. 2. *Pelmatochromis ocellifer*, from Boulenger, 1915 fig. 264.

Series of scales on cheek 3–4; scales between origin of dorsal and lateral line $2\frac{1}{2}$–3. Anal fin-rays III 7–8. Vertebrae 26 (3 specimens x-rayed).

In some specimens one or more dark horizontal streaks on anterior part of body, the uppermost above and on the upper lateral line, others uneven, below it (see fig. 2). Five broad dark vertical bars present or absent.

Known from three localities in the Congo basin—Monsembe on R. Congo, Karawa on a tributary of R. Mongala and R. Ja.

P. nigrofasciatus

Paratilapia nigrofasciata Pellegrin, 1900 : 353 (Nganchou, Congo, not far downstream from Kasai-Congo confluence).

Pelmatochromis nigrofasciatus (part.); Pellegrin, 1904 : 280, pl. vi fig. 2.

Pelmatochromis ocellifer (nec Boulenger); Steindachner, 1914 : 57 fig. 12 (R. Ja); Gosse, 1963 : 230; Thys van den Audenaerde, 1967 : 93; id. 1968a : fig. 13.

Paratilapia longipinnis Nichols & Griscom, 1917 : 728 fig. 29 (Congo at Coquilhatville and Irebu).

Teeth (fig. 4). In a young fish of SL 22 mm only one row of teeth is present in the lower jaw and some of these are notched, others have one cusp and a shoulder; there are only a few upper inner teeth, and these (and others when they develop) have one sharp cusp and a pair of shoulders; most of them retain this shape but from SL about 100 mm some of them are replaced by conical teeth. Already at SL 38 mm there are no more notched teeth in the outer series, but the teeth are still flattened in section and shouldered; later the shoulder is lost and more and more of the outer teeth become conical. The last to retain a shoulder are the lateral teeth of the lower jaw, where the band may be a little wider and the teeth overlap obliquely; in large specimens these too become conical.

The outer teeth are more numerous and close-set than in *P. ocellifer*, 54 64 in the upper jaw, 74 in a specimen of SL 116 mm. There are 4 rows in the upper jaw,

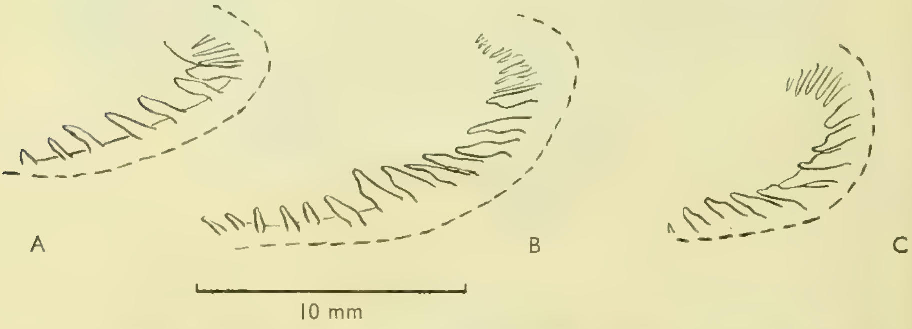


FIG. 3. Outer gill-rakers of first arch in, A, *Pelmatochromis ocellifer* of SL 100 mm, B and C, *P. nigrofasciatus* of 109 and 61 mm respectively.

3 in the lower, unevenly broadening to an extra row in both jaws in large specimens, and the inner are much smaller than the outer.

Premaxillary pedicels 21·6–26·8% length of head (27·7 in one), interorbital width 33·5–38·0.

Gill-rakers on first arch (4–8) + 1 + (8–14), the upper very slender (fig. 3). Pad on roof of pharynx moderate, a shallow groove in front of it.

Lower pharyngeal bone slender, with all the teeth very slender, up to twice as many in a middle row as in a comparable specimen of *P. ocellifer* (fig. 5). In a young fish of SL 61 mm there is a total of about 135 teeth on the bone as compared with 120 in a 64·5 mm *P. ocellifer* and 110 in the 100 mm specimen of that species.

Scales of cheek in 3 rows, between origin of dorsal and lateral line 3½–4. Anal III 9–10. Vertebrae 26 (f.4) or 27 (f.1); in the last, one vertebra has an abnormally short centrum.

A scaly sheath at base of anal fin. Rows of small scales along the caudal rays for ¼ to ½ of their length.

Colour in alcohol: Six dark vertical bands of varying intensity on the body, the first immediately behind operculum, the last at the ene of caudal peduncle, these bearing up to six large, round blotches in series from behind opercular spot to end of caudal peduncle; of ten a faint or incomplete upper band or series of blotches. In a few specimens upper end of transverse band immediately below the tilapia-mark intensified, suggesting a "pelmatochromis-mark" like that characteristic of *P. buettikoferi*. Tilapia-mark becoming smaller in adult and finally vanishing or obscured by general dark colour of fin. Some individuals with alternate dark and clear spots on caudal and soft dorsal and a white upper edge to dorsal fin.

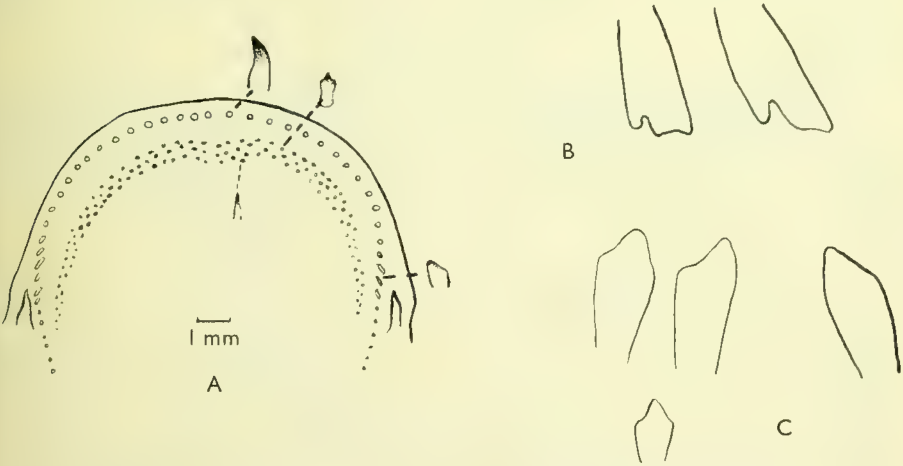


FIG. 4. *P. nigrofasciatus*. A. Plan of dentition of lower jaw in a fish of SL 120 mm. B. Two outer teeth of a juvenile of SL 22 mm. C. Three outer and one inner teeth of a juvenile of SL 35 mm.

Colour in life: In the young male described by Matthes (1964) the vertical bands and blotches were present but rather faint, the upper edge of the dorsal was yellow and series of spots were black on the anterior part of the fin, red on the posterior rays. The anal bore black spots proximally, red distally on a yellow ground. The outer rays of the pelvics were black, inner yellow. Filamentous tips of dorsal, anal and pelvics were black.

The diet (Matthes, l.c.) is predominantly vegetable, the stomachs of the two specimens examined by Matthes containing masses of filamentous and unicellular algae as well as insect remains and mud.

Reproduction. Gosse records that it is a substrate-spawner and guarder of the brood.

Natural distribution: throughout the central Congo basin from Yangambi to Kinshassa, including R. Rubi, R. Chuapa, R. Ja and the Kasai.

Pellegrin's description of the types is in agreement with this rather than with *P. ocellifer* in the following details:- gill rakers "une dixaine a la partie inferieure au premier arc branchial"; 9 soft rays in the anal fin; six broad transverse bands on the body; teeth small and "peu distinctes", the outer a little longer than the inner. All these details are confirmed by my notes on the types, in which I found 9 gill-rakers on the lower part of the arch, excluding one at the joint.

Steindachner evidently had both species but transposed their names, calling the one with the narrower interorbital and 8 gill-rakers *P. nigrofasciatus*, the one with the wider interorbital and five dark spots of unequal sizes on the flank *P. ocellifer*. He described under *P. ocellifer* a dentition perfectly corresponding to that found in *P. nigrofasciatus* described above, including the broadening of the lower band near the corner of the mouth. The inner teeth are described as "winzig" and the outer as not insignificantly bigger than the inner. A discrepancy is the ascription of 5 rows of cheek scales to this species, but his figure shows only three and is a recognizable *P. nigrofasciatus*.

This is the only record of the species in R. Ja, a secondary tributary of the Congo.

Pellegrin (1931 : 211) and Daget (1961 : 585) record *P. nigrofasciatus* from the Niari-Kouilou and we have one at the BM (NH) collected by M Ch.Roux near Point Noir. They are more slender (depth 33–40% SL) but otherwise agree with the Congo specimens.

THE STATUS OF *PELMATOCHROMIS EXSUL*

Having corrected a misidentification of Dr Poll's, I have now to correct a more serious one of my own.

Pelmatochromis exsul Trewavas: (1933 p. 320, fig. 4) was described from 3 small specimens, 25·5+6·5 to 34·5+10 mm long, from Lake Rudolf. On re-examining them I have come to the conclusion that they are young *Hemichromis bimaculatus* Gill, 1863. Unlike all our preserved specimens they have no distinct black spot on the flank. I have looked at the base of the skull in one and find that its apophysis for the upper pharyngeal bones is so little developed that it could hardly be used for diagnosis, but it might well be of the *Hemichromis* type. Numbers of scales, finrays and gill-rakers are in agreement with *H. bimaculatus* and the arrangement of the circuli of the scales is gothic (see p. 14 and fig. 10).

This species occurs in the Nile, whence the fish-fauna of Lake Rudolf is derived, and although it has not been caught in subsequent collections from the lake it is probably there in suitable habitats.

This correction removes an apparent anomaly in the distribution of *Pelmatochromis.*

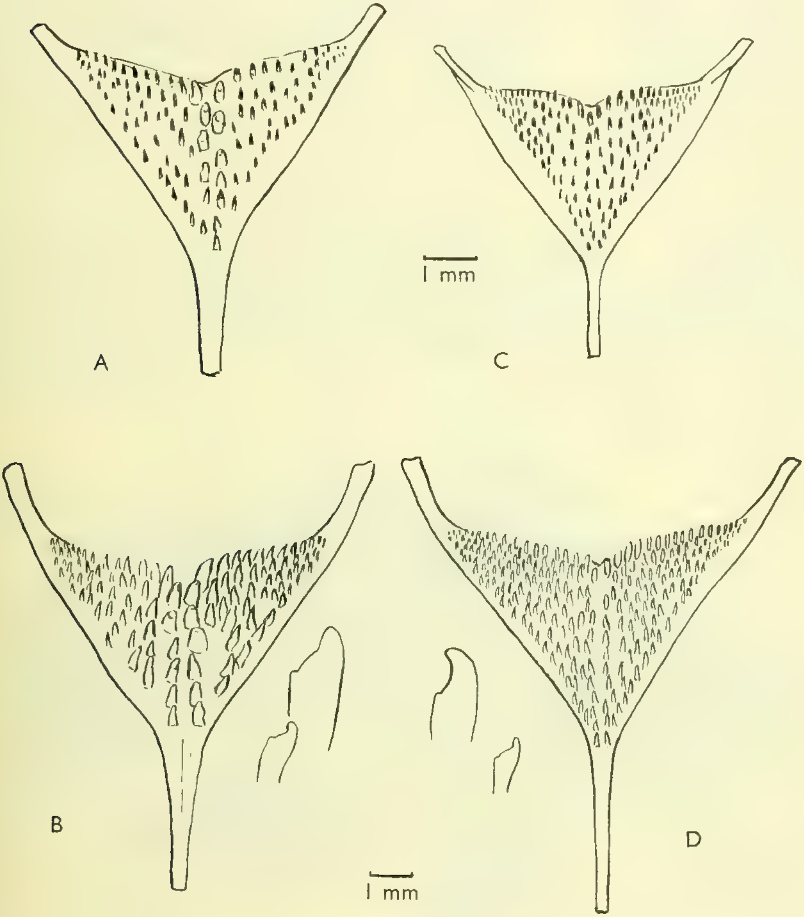


Fig. 5. Lower pharyngeal bones of *Pelmatochromis ocellifer*, A, at SL 64 mm, B, SL 100 mm; and *P. nigrofasciatus*, C, at SL 61 mm and D, SL 116 mm. A middle posterior tooth and an anterolateral are shown enlarged for each of the adult fishes.

INTERRELATIONSHIPS OF THE SPECIES OF *PELMATOCHROMIS*

It is to *P. nigrofasciatus* and not *P. ocellifer* that Thys is referring when he writes (1968a) that *P. congicus* is a specialized form derived from *P. ocellifer*. With the substitution of the name I would agree with this opinion, but the specialization has gone so far that *P. congicus* is best considered as a separate genus.

P. ocellifer and *P. buettikoferi* are alike in the dentition of jaws and pharynx in which they contrast with *P. nigrofasciatus*, especially developmentally. On the other hand *P. buettikoferi* differs from both Congo species in the colour-pattern, having no tilapia-mark, but instead a dark spot on the back below the site of the tilapia-mark of others, and its pelvic, dorsal and anal fins are less produced. *P. ocellifer* has a shorter series of epibranchial gill-rakers on the first arch than either of the other two species. Some other aspects of their structure will be considered in discussing their alleged relationship with *Tilapia*.

I propose a new genus, *Pterochromis*, for the type species *P. congicus* Boulenger, distinguished from *Pelmatochromis* by its large oblique mouth, long slender gill-rakers and more specialized dentition. The two genera have in common the following features:-

Apophysis for the upper pharyngeals formed by the parasphenoid alone; all teeth unicuspid in adult; pad on roof of pharynx sessile; microbranchiospines present; lateral lines overlapping by only one or two scales if at all, the upper separated from the dorsum posteriorly by $1\frac{1}{2}$ scales; scales cycloid, partly roman, partly gothic (see fig. 10).; vertebrae 26 or 27, mode 26; scales 27 or 28 in lateral line series.

They are distinguished from each other as follows:-

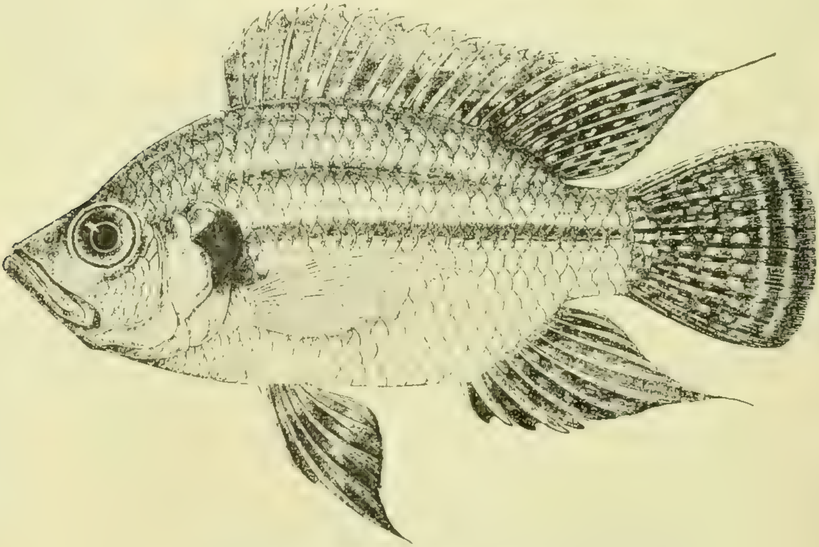


FIG. 6. *Pterochromis congicus* from Boulenger, 1915 fig. 261.

PELMATOCHROMIS Steindachner

Lower jaw 35–42% length of head, premaxillary pedicels 21½–33%; mouth at an angle of 20–40° with the horizontal; gill-rakers (2–8) + 1 + (6–14) on first arch.

Three species, *P. buettikoferi*, *P. ocellifer*, *P. nigrofasciatus*.

PTEROCHROMIS n. gen.

Type *Pelmatochromis congicus* Boulenger = *Pterochromis congicus*.

Lower jaw 51–54½% length of head, premaxillary pedicels 42–43½%; mouth at an angle of 40–50° with the horizontal; gill-rakers (9–11) + 1 + (17–19) on first arch (fig. 3).

A single species.

Pterochromis congicus

Pelmatochromis congicus Boulenger, 1897 : 422 (Stanley Falls); id. 1898 : 149; id. 1901 : 437 (Stanley Falls and L. Obéké); Pellegrin, 1904 : 287; Boulenger, 1915 : 386, fig. 261; Thys van den Audenaerde, 1968a : 371, fig. 14 (after Boulenger).

The measurements in the generic definition have been taken from 5 specimens of SL 58–152 mm including the holotype, a specimen from L. Obéké and 3 from R. Momboyo.

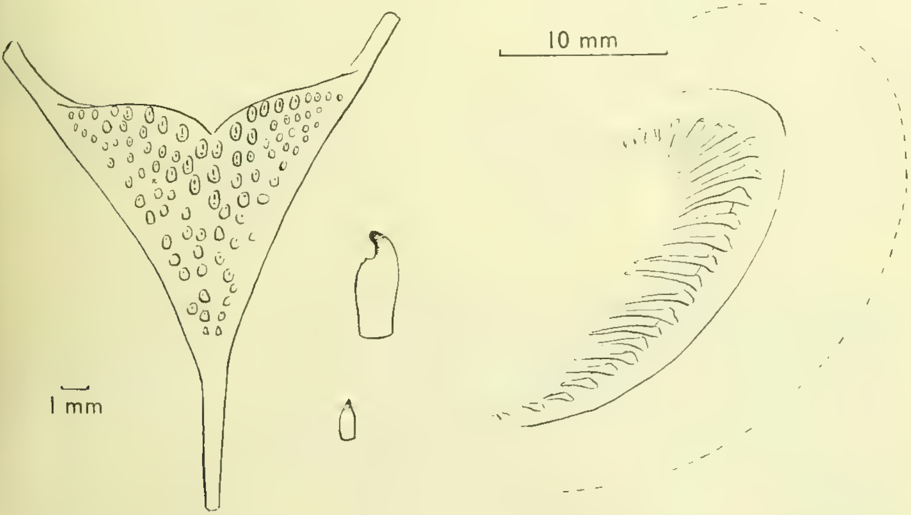


FIG. 7. *Pterochromis congicus*, lower pharyngeal bone with isolated posterior and anterior teeth; and rakers of first gill-arch in a specimen of SL 150 mm.

Dentition. In the 68 mm specimen all the teeth are unicuspid with no shoulder. In the 68 and 71 mm specimens there is only one, irregular inner row, of few, very small teeth; in the 71 mm fish I cannot find any inner teeth in the upper jaw. At SL 150 mm there are 1–2 irregular rows of inner teeth in the upper jaw, 2 in the lower. In all the outer teeth are conical, firm, the two or three anterior on each side in the lower jaw spaced and thicker than the rest. In the 150 mm fish the tooth-band of the lower jaw is broadened anteriorly by wider spacing between the rows (fig. 8).

There is no evidence of a pluricuspid stage. Both this species and *Pelmatochromis nigrofasciatus* have a characteristically pigmented tooth-bed in which each inner tooth pierces a tiny pigment-free disc.

The pharyngeal teeth are narrow but rather coarse, the posterior bicuspid, the anterior conical. (fig. 7).

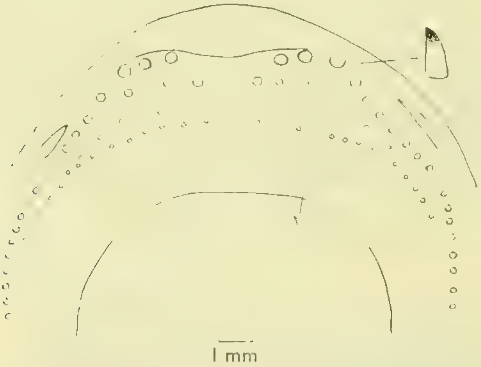


FIG. 8. *Pterochromis congicus*, SL 150 mm, plan of dentition of lower jaw and isolated outer and inner teeth to the same scale.

KEY TO THE SPECIES OF ***PELMATOCHROMIS***

1a Outer teeth unicuspid in adult, shouldered in juveniles, some notched in very young; inner much smaller than outer, some retaining minor cusps in adult, others replaced by unicuspids; premaxillary pedicels 21·5–27·7% length of head; gill-rakers 8–14 on lower part of first arch; a tilapia mark Congo . ***nigrofasciatus***

1b Teeth unicuspid, curved cones at all known stages, inner shaped as outer and only a little smaller; premaxillary pedicels 27·7–33·0% length of head; gill-rakers 6–8 on lower part of first arch . . . . 2.

2a A tilapia-mark; lower jaw 35–38% length of head; 2 or 3 epibranchial gill-rakers. Congo . . . . ***ocellifer***

2b No tilapia-mark in adult, but a black spot on the back below junction of spinous and soft dorsal, lower jaw 38–42% length of head; 3–6 epibranchial gill-rakers. Liberia to Sierra Leone . . . . ***buettikoferi***

THE RELATIONSHIP BETWEEN *PELMATOCHROMIS* AND *TILAPIA*

To include as Thys (1968b : xxvii–xxix) does *Pelmatochromis buettikoferi, P. ocellifer, P. nigrofasciatus, Pt. congicus* and *Tilapia busumana* in the same subgenus requires a definition full of alternatives. I will proceed to examine the characters on which he relies and some others that seem to me to be relevant to the relationship.

Dentition of jaws

We have no *P. ocellifer* smaller than 63 mm SL and in this the teeth are unisucpid, curved cones of the adult type. The same is true of the smallest *P. buettikoferi* examined, a specimen of 28 mm SL. The teeth of *P. nigrofasciatus* from SL 22 mm to the adult have been described on p. 6 and fig. 4.

The only species of *Tilapia* in which the very early development of the teeth has been described is *T. tholloni*. Fishelson (1966 : 197) states that they are unicuspid at first appearance, but at the 15th day after fertilization there are already tricuspid teeth. In his fig. 23 of a 16-day larva one minor cusp is visible on each clearly defined tooth. This goes on to develop into the well-known *Tilapia* dentition, with bicuspid outer and tricuspid inner teeth.

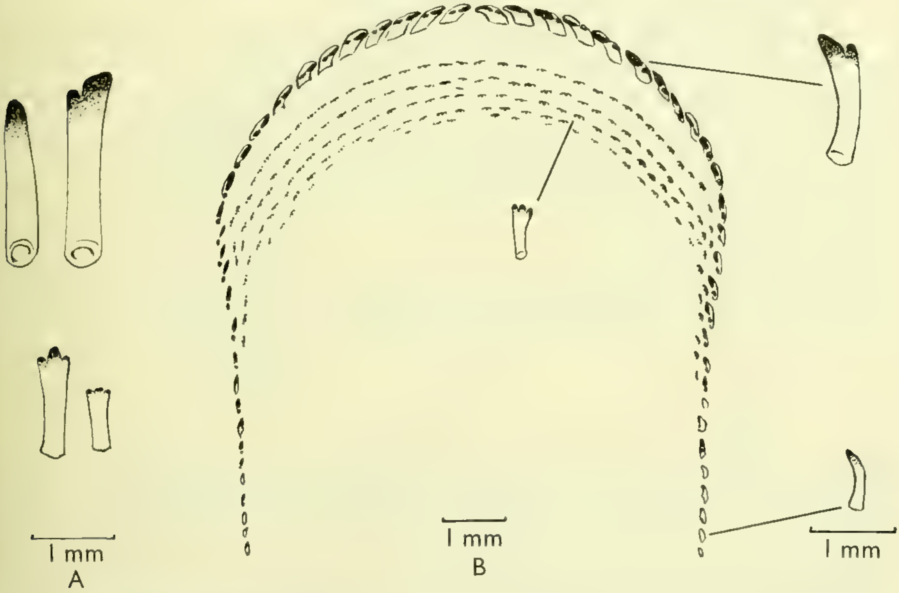


FIG. 9. *Tilapia busumana*, A, isolated teeth from a specimen of SL 156 mm; above, one of the 22 outer lateral simple teeth from right ramus of upper jaw and one of the 11 bicuspid anterior outer teeth from the same; below, inner teeth from respectively the row next to the bicuspids and the inmost row; the open lower ends of the outer teeth are seen because of the curve of the axis of each in a plane at right angles to the page. B, dentition of lower jaw, with enlarged drawings of three of the teeth in a fish of SL 111 mm.

In *T. busumana*, where in the advanced adult progressively more of the lateral teeth become replaced by strong unicuspids, the anterior retain a minor cusp and the inner, at first with three subequal cusps, retain two reduced minor cusps (fig. 9). Up to SL 110–120 mm there is a typical *Tilapia*-dentition of bi- and tricispid teeth, the inner still with three subequal cusps and only 7 or 8 unicuspids at the ends of the outer row of the upper jaw.

In the Zambezi populations of *Tilapia ruweti* (Poll & Thys) some of the teeth become pointed in adults by reduction in the anterior or suppression in the posterior teeth of the minor cusps.

The food of these two species of *Tilapia* has not been fully studied, but by analogy it may be supposed that the teeth of *T. ruweti* become adapted to seizing small invertebrates, which perhaps form an increasing part of the diet as the fish grows. The lateral unicuspids of *T. busumana* are in the wrong position for seizing and are more likely to act as a barrier to prevent loss of food items taken in at the front of the mouth (c.f. the dentition of *Pseudotropheus*, *Tropheus* and *Simochromis* of Lakes Malawi and Tankanyika).

Thus we have four types of dentition in the species under consideration:-

(1) Outer and inner teeth curved, conical at all stages (from SL 28 mm). ***P. buettikoferi*, *P. ocellifer*.** (and *Pterochromis*)

(2) Outer teeth notched or shouldered in the very young, then shouldered, then conical; inner shouldered, then mixed shouldered and conical, then conical, much smaller than outer. ***P. nigrofasciatus*.**

(3) Teeth pluricuspid at first, becoming pointed in adult by reduction or, in some teeth, suppression of the minor cusps. Some individuals of ***Tilapia ruweti*.**

(4) Outer teeth bicuspid, the lateral replaced in large individuals by strong conical teeth; inner tricuspid, the lateral cusps reduced in fishes of 130 mm or more. ***T. busumana*.**

The differences, examined closely, are such as to need overwhelming support from other characters before either species of *Tilapia* in united in one subgenus with *Pelmatochromis*, and the position of *P. nigrofasciatus* in relation to both genera requires scrutiny.

Scales

In African Cichlidae there is considerable diversity in the structure of the scales. Leaving out of consideration the ctenoid scales of the *Haplochromis* group, there are in West Africa two main types of cycloid scales based on the arrangement of the circuli. I name them by analogy with architectural arches roman and gothic. In roman scales the circuli in the posterior field are parallel to the edge, in gothic they meet at an angle (fig. 10). All the scales are gothic in *Hemichromis* and in *"Pelmatochromis" thomasi* Boulenger (not a true *Pelmatochromis*). *Pelmatochromis buettikoferi, P. ocellifer, P. nigrofasciatus and Pt. congicus* all have a mixture of gothic and roman, except in adult *Pt. congicus*, where all are roman. In *T. busumana* and all the species of *Tilapia* except *T. ruweti* (Poll and Thys) all the scales are roman. In both *Pelmatochromis* and *Tilapia* a large part of the posterior field of many of the scales may become granular, so that the circuli are partly obliterated, but it is generally possible to see the direction of the circuli from the other part of the scale. *Tilapia ruweti* is one of the species having a granular area in many scales; where the circuli are complete they are either roman or gothic, in the latter case the angle at which the circuli meet is blunt, represented by a narrow curve.

Vertebrae (Table I.)

In African Cichlidae it may be accepted that low numbers of vertebrae are primitive except where numbers are secondarily reduced in waters of high temperature. In the three species of *Pelmatochromis* taken collectively the modal number is 26. The only *Tilapia* having the same mode is *T. guinasana,* which Thys has placed in a separate subgenus* on account of its large scales. *T. busumana* agrees with the type-species of *Tilapia* in having a strong mode at 27. In *T. zillii* (and other species of the subgenus *Coptodon* except *T. rendalli*) the mode is 28.

Parenthetically, the three specimens of *P. buettikoferi* with 26 vertebrae are from Liberia, near the type-locality, the three with 27 from Sierra Leone and R. Corbal, the latter the type of *P. corbali* Boulenger, regarded as a synonym. Only more data can determine the significance, if any, of this.

TABLE I. Frequencies of vertebral numbers in *Pelmatochromis, Pterochromis* and species of *Tilapia*

Number of vertebrae	26	27	28	29
Pelmatochromis				
P. ocellifer	3			
P. buettikoferi	3	3		
P. nigrofasciatus	4	1		
Pterochromis				
P. congicus	2			
Tilapia				
T. ruweti		3		
T. sparrmanii	1	10	5	
T. busumana	1	25	2	
T. guinasana	11			
T. zillii		5	33	2

The tilapia-mark

The tilapia-mark, a black spot, often surrounded by a transparent or yellow ring, at the junction of spinous and soft parts of the dorsal fin, is, as its name indicates, very characteristic of the species of *Tilapia* and *Sarotherodon***; either throughout life or in juveniles. But it turns up too in other, related genera, derivatives as I interpret it of the source-group of *Tilapia.* Among these it is more sporadic than in *Tilapia* or *Sarotherodon.* So, in *Pelmatochromis* it is present in *P. ocellifer,* absent in *P. buettikoferi. P. nigrofasciatus* and *Pt. congicus* have a tilapia-mark in the young and this becomes drawn out in a direction parallel to the fin-rays and then disappears in the adult. In young *Chromidotilapia* sp. of West Cameroon there is a similar mark and the females of *C. batesii* have a more vaguely defined mark in the same position. In *Stomatepia mariae* of Barombi Mbo, a species with a predacious habit and aspect, there is a typical tilapia-mark in the young, becoming elongate and drawn out parallel to the rays in the adult and finally vanishing. On the other hand, of two sibling species of *Sarotherodon* in Barombi Mbo, one has a conspicuous tilapia-mark in the young, the other has none. Young of *Leptotilapia irvinei* have a tilapia-mark (Roman, 1966).

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* The name *Trewavasia* proposed for this subgenus by Thys is preoccupied.

** Until now considered a subgenus of *Tilapia.* I consider it worthy of generic rank. See p. 20.

In short, the presence or absence of a tilapia-mark is not absolutely diagnostic of these genera, although it must be taken into account in assessing relationships.

A colour feature in *T. busumana*

The postero-dorsal corner of the caudal and the tip of the soft dorsal in *T. busumana* are narrowly margined with white or red according to the environment. Although this is a common pattern in *Chromidotilapia* (and *Pelvicachromis* Thys), *T. busumana* is not the only *Tilapia* exhibiting it. It is found too in *T. louka* Thys and *T. mariae* Boulenger.

Length of intestine

In a *P. buettikoferi* of 74 mm SL the intestine is about 2·3 times the SL, in a *T. busumana* of 76 mm it is 2·5 times this length. This is short for *Tilapia* and is

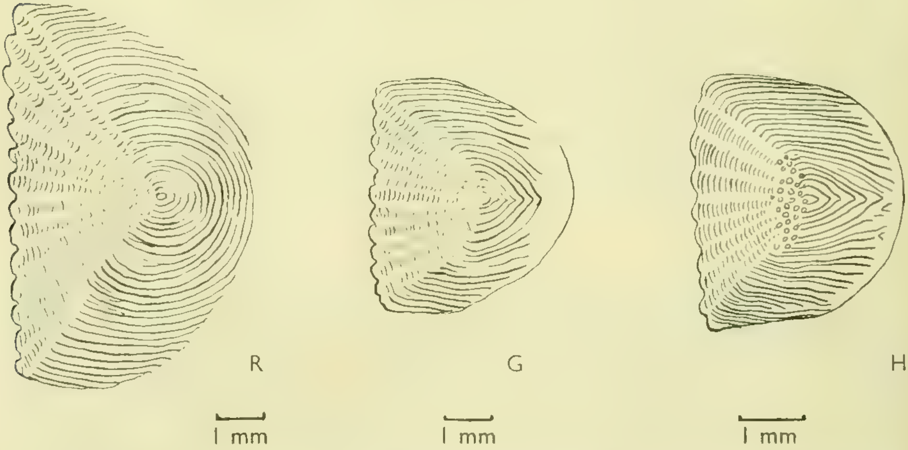

FIG. 10. Scales from between the anal fin and the lateral line in R, *Tilapia busumana* (roman) and, G, *Pelmatochromis buettikoferi* (gothic). In *T. busumana* the circuli are more numerous and close-set than in the drawing. For comparison, H, a flank scale of *Hemichromis bimaculatus* (gothic).

in line with the changed dentition and presumably diet in adult *T. busumana*. It is a feature in which this species resembles *Pelmatochromis* more than other species of *Tilapia*.

The epibranchial structures

Glandular and sensory pads on the roof of the pharynx are present in most (all?) cichlids anterolaterally to the upper pharyngeal teeth.

When Steindachner proposed the subgenus *Pelmatochromis* (Gr. pelma, gen. pelmato = the sole of the foot, referring to the shape of the pad) he included two species, *P. buettikoferi* and *P. jentinki*, without designating either as type. Regan (1922) used the criterion of page priority to designate *P. buettikoferi* as type-species, and this is the one in which the pad is not boot-shaped, as Steindachner knew. Pellegrin, Boulenger and Regan eventually considered *Pelmatochromis* to include also *Chromidotilapia* Boulenger, 1898 (type *C. kingsleyae*), finding a gradation between the extreme shapes of the pad. Thys (1968a) has revalidated *Chromidotilapia* for species with a boot-shaped pad, since in this group its presence or absence is correlated with the respective absence and presence of microbranchiospines. This seems to be a natural division, although that the correlation is not always functionally or genetically necessary is shown by the fact that *Tylochromis* and *Callochromis*, for instance, have both a boot-shaped pad and microbranchiospines.

Thys stated (1968a : 374) that the projecting pad is a glandular sac with an opening on each side in front of the upper pharyngeal tooth patches. This I

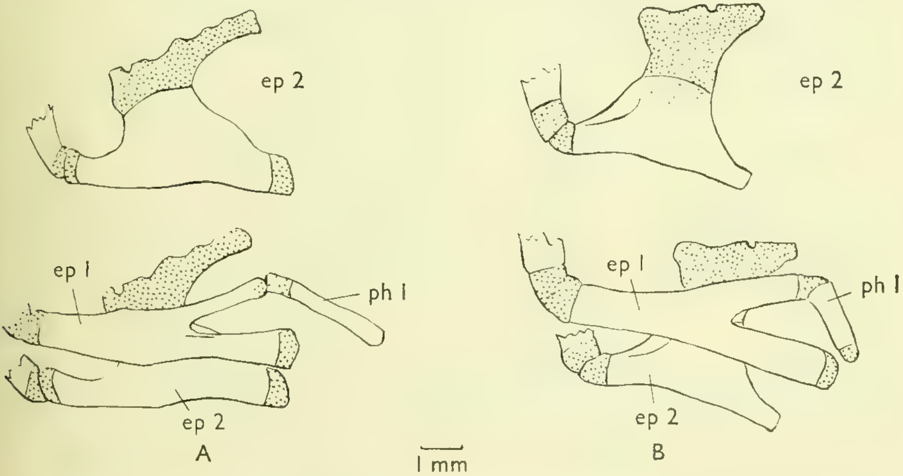

Fig. 11. Upper bones of 1st and 2nd branchial arches in, A, *Tilapia busumana*, B, *Pelmatochromis nigrofasciatus*. The bones are drawn as if detached from the skull and viewed from above. Cartilage dotted. *ep* 1, *ep* 2, 1st and 2nd epibranchial; *ph* 1, 1st pharyngobranchial. The 2nd pharyngobranchial, a small toothed bone, is not shown.

cannot confirm by examination with a dissecting microscope for either the boot-shaped or the sessile pad, and Thys gave no evidence for his statement. Dissection of both the hanging and the sessile pads reveals only connective tissue inside, often fat-laden. In the midst of this is a lamina of cartilage and bone that is an expansion of the anterior edge of the second epibranchial (fig. 11). On the oral side the membrane is raised into ridges and bosses bearing sensory cells. The histology of these pads has been little studied. Al Hussaini & Kholy (1954) found in the pharynx of *Tilapia nilotica* columnar cells interspersed with granular cells. Stolk (1957) described secretory cells in the pads of female *Haplochrmis multicolor* without comparing them with the males. Fishelson (1956 : 588, fig. 19) demonstrated both glandular and sensory cells in *Tilapia tholloni* not only between and beside the upper pharygeal tooth-plates, but also on the floor of the pharynx, including the gill-arches.

Macroscopically the pad is very similar in *Pelmatochromis* and *Tilapia*, but between *Tilapia* on the one hand and two of the species of *Pelmatochromis* (and *Pt. congicus*) on the other there is a difference in the epibranchial structures. In these (*P. buettikoferi* and *P. nigrofasciatus*) as also in *Chromidotilapia*, there is a long series of slender epibranchial gill-rakers on the first arch and the fold of skin (frenum) at the hinge between suspensorium and epibranchial is remote from the epi-ceratobranchial joint. This leaves a free passage for a current, respiratory or food-bearing, to pass between the pharynx and the upper part of the parabranchial chamber, in which direction can only be tested by experiment (fig. 12A).

In *Tilapia*, on the other hand, the epibranchial gill-rakers are few, short and blunt and the frenum is attached near the epi-ceratobranchial joint. The upper gill-filaments are attached along a line turning inwards behind the frenum, which would obstruct any flow of water between the upper filaments and the pharynx (fig. 12B).

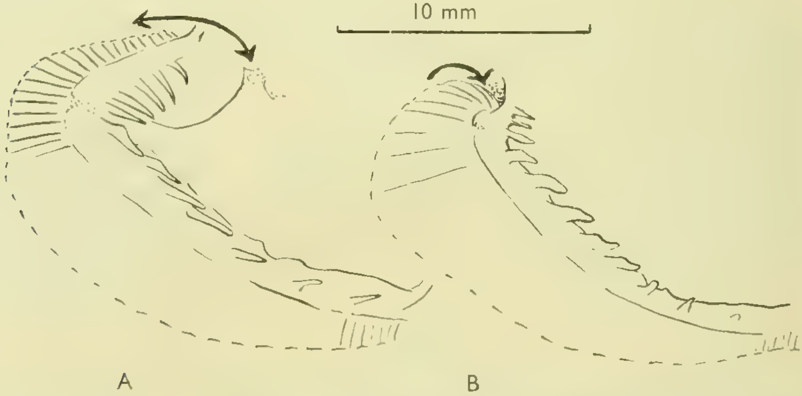

FIG. 12. Outer gill-rakers of first arch in, A, *Pelmatochromis buettikoferi* of SL 98 mm, B, *Tilapia busumana* of SL 91 mm. The arrows show possible directions of the current in the upper part of the gill-chamber.

P. buettikoferi and *P. nigrofasciatus* have a transverse groove on the roof of the pharynx between the top of the first epibranchial and the middle of the pharyngeal roof. This is less sharply demarcated than a similar groove in the cichlids with the hanging pad, but the groove and the free epibranchial passage must together influence the currents at the back of the pharynx, which can hardly be the same as those of *Tilapia* and other genera with an obstructing frenum and no transverse groove.

Pelmatochromis ocellifer, in the few, rather damaged specimens at our disposal, seems to have an epibranchial region more like that of *Tilapia* than the other species of *Pelmatochromis*, although in other respects it resembles the latter.

CONCLUSIONS ON *PELMATOCHROMIS* AND *TILAPIA*

The only species of *Pelmatochromis* showing any evidence of derivation from an ancestor with a *Tilapia*-like dentition is *P. nigrofasciatus*. The fact that the outer teeth are notched only at such an early stage that they can hardly be functional as such suggests that they are a vestigial feature derived from an ancestor that had indeed a *Tilapia*-like dentition. That the ancestor was a *Tilapia* may be doubted because of the epibranchial structures and there is no evidence at all of such an ancestral dentition for *P. buettikoferi* and *P. ocellifer*. The adult dentition of *P. nigrofasciatus* is itself so distinct as to suggest that *Pelmatochromis* is diphyletic. If this is so, it will not, in my opinion, be mended by putting *P. nigrofasciatus* in *Tilapia*, although the two (?) ancestral species of *Pelmatochromis* and the one (?) of *Tilapia* must have been rather closely related. Any opinion as to whether *Tilapia* and *P. nigrofasciatus* can be traced back to a single ancestor that was already separate from the ancestor of *P. buettikoferi* and *P. ocellifer* must be purely speculative. The creation of a separate genus for *P. nigrofasciatus* would express both our guesses and our doubts, but the purpose of genera is not solely to express the speculations of taxonomists (although we endeavour not to allow them to cut across the more firmly based of these) and I propose to leave *P. nigrofasciatus* in *Pelmatochromis* with the above qualifications.

On both geographical and structural grounds the *Tilapia* coming nearest to *P. nigrofasciatus* is *T. ruweti*, of swampy pools and streams on either side of the Congo-Zambezi water-shed. It was originally described as a *Pelmatochromis* because of its rounded caudal and its spotted, showy vertical fins. This, however, is *Tilapia*-like in its few (2–3, usually 2) short epibranchial gill-rakers, 27 vertebrae and its dentition and it so closely resembles *Tilapia sparrmanii* as to be difficult to distinguish from it even in life.

As for *T. busumana*, this has a functional *Tilapia*-dentition far into adult life and the replacement of its lateral teeth by unicuspids is probably not a strictly parallel event to the development of the adult dentition of *P. nigrofasciatus*. Functionally it cannot serve the same purpose (p. 14). A more exact parallel is found in the transformation that occurs in adult males of *Sarotherodon angolensis* Trewavas (p.29 below). The relationship of *T. busumana* with its geographical neighbour *P. buettikoferi* is not very close, perhaps at the subfamilial level, although other genera must be taken into account (including the South American) before subfamilies can be established with confidence within the Cichlidae.

STATUS AND DEFINITION OF *TILAPIA* AND *SAROTHERODON*

During recent years information has been accumulating on the species of *Tilapia* in the broad sense to show that on both structural and behavioural features they fall into two well-defined groups. Thys van den Audenaerde (1968) has indeed recognised three "Sections", but the first two fall together on their reproductive pattern and the structures associated with it. The earliest name of the genus-group for the species of Thys's sections I and II is *Tilapia* A. Smith, 1840, for his section III *Sarotherodon* Rüppell, 1853. In 1968 Thys left the latter as a subgenus of *Tilapia* (as it was used by Regan in 1920 and Trewavas in 1966), but in 1970 (p. 295) he writes of *Coptodon* Gervais (while listing it as a subgenus of *Tilapia*) that it and *Sarotherodon* are "major subgenera, in fact good genera". In 1971 he again uses it as a subgenus.

I cannot find any good reason for regarding *Coptodon* as more than subgenerically distinct from *Tilapia*, but if Thys means to say that *Tilapia* and *Sarotherodon* are to be regarded as genera I would agree with him and have now adopted this usage (Trewavas, Green and Corbet, 1972). Their principal characters have been described by Lowe (1959) and Peters (1961) and again by Thys (1970). Some of the differences between *Coptodon* and *Sarotherodon* given by Thys do not distinguish all species of *Tilapia* (or *Coptodon*) from *Sarotherodon*, and even if one selects the most reliable, exceptions must be admitted. I would prefer to postpone my full definitions to a publication containing all the evidence in the form of specific descriptions, but in the hope of avoiding confusion I give what appear to be the most generally verified distinctions.

Tilapia

1. Gill-rakers 7–16 on the lower part of the first arch, more than 12 in only the three species of subgen. *Pelmatolapia* Thys.
2. Median length of lower pharnygeal bone 21·5–28·5% length of head (rarely up to 30·5 in *T. rendalli*).
3. Pharyngeal blade/median length of toothed area 0·3–0·75 (0·5–1·0 in *T. mariae*).
4. Mesethmoid meeting vomer in all except one species (*T. rendalli*) and some individuals of *T. dageti*, *T. guineensis*, *T. discolor*, and *T. zillii* (fig. 13).
5. Substrate spawners and guarders of the brood.

Sarotherodon

1. Gill-rakers on lower part of first arch 10–28, less than 13 in only three species.
2. Median length of lower pharyngeal bone 27·5–43·5% length of head in adult.
3. Pharyngeal blade/median length of toothed area (0·4) 0·8–3·5.
4. Mesethmoid not meeting vomer (fig. 14).
5. Mouth-brooders.

Comments on the distinguishing characters

The species of *Sarotherodon* with fewer than 13 gill-rakers in some individuals are *S. franchettii*, *S. alcalicus* and *S. amphimelas*, all inhabiting specialized biotopes.

The median length of the pharyngeal bone (as % length of head) increases with size of fish, especially in *Sarotherodon*, and in the majority of species of this genus it is 30% or more in adults. In a few the minimum length is below 30%, but (except in *S. percivali*) the maximum always exceeds 30%, even in such small species as *S. alcalicus* and *S. franchettii*. Of the species that grow to a good size the lowest range (25·5–31·5%) is found in *S. aureus*, nearly approached by *S. pangani*.

The species of *Sarotherodon* that have the pharyngeal blade often a little shorter than the toothed area in adults are *S. niloticus*, *S. aureus*, *S. urolepis*, *S. placidus*, *S. andersoni* and the three species of the Pangani system. The exceptionally short ratio of 0·4 occurs in *S. pangani girigan*, in which the toothed area is enlarged and the teeth are unusually coarse. In this category too comes *S. steinbachi* of Barombi Mbo, in which although the whole bone is very long and the teeth fine and crowded the toothed area is enormously enlarged.

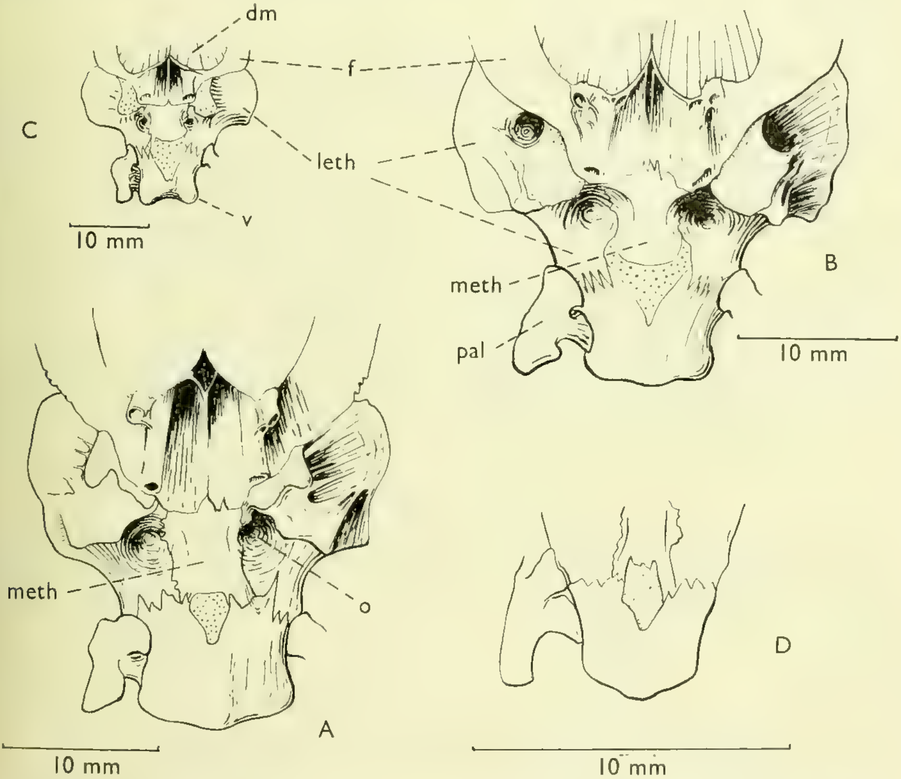

FIG. 13. Ethmovomerine region in *Tilapia*. A, *T. zillii* of SL 205 mm, Nile, B, *T. rendalli* of SL 200 mm, Lake Malawi, C, *T. dageti* of SL 170 mm, Gambia, D, *T. mariae* of SL 86 mm, Lake Barombi Kotto. Cartilage dotted, *dm* dorsal muscles, *f* frontal, *leth* lateral ethmoid, *meth* mesethmoid, *o* olfactory foramen, *pal* head of palatine, *v* vomer.

The ethmo-vomerine relationship is illustrated in figs 13 and 14. The vomer surrounds the rostral end of the ethmoid cartilage and laterally makes a sutural union with the lateral ethmoid at the articular surface with the upper arm of the head of the palatine. In most cichlids (and other Perciformes) the mesethmoid ossification meets the vomer dorsally between these two points, forming a complete or nearly complete bony roof for the ethmoid cartilage. This is true of *Pelmatochromis*, *Chromidotilapia* and the genera of the *Haplochromis*-group and also of *Tristramella* and most species of *Tilapia*, in which there is a small area of cartilage left free between right and left ethmo-vomerine sutures (fig. 13). But in *T. rendalli* (3 specimens tested) the anterior edge of the mesethmoid is rounded and free from the vomer. It was the contrast between *T. rendalli* on the one hand and *T. zillii* and *T. busumana* on the other that led Regan (1920) to recognize the subgenus *Coptodon* for *T. zillii* and *T. busumana*. Regan did not then know that the ethmo-vomerine sutures characterize also the type species of *Tilapia*, *T. sparrmanii* A. Smith.

We do not now consider it possible to separate *T. zillii* and *T. rendalli* subgenerically. Although the ethmo-vomerine union cannot be used as an absolutely diagnostic feature of *Tilapia*, its opposite, the freedom of these bones from each other, appears to be a constant feature of *Sarotherodon*, verified by me in at least one specimen each of fourteen species. *Sarotherodon* is specialized in this respect as also in its dentition, especially the pharyngeal, and in its reproductive arrangements.

One may suggest a possible functional explanation for the failure of the mesethmoid to meet the vomer in *Sarotherodon*. These predominantly microphagous species are characterized by a very broad head, providing a long and broad buccopharynx for the passage of large quantities of food-laden water. At the same time the stresses and strains on the jaw apparatus are far less than they would be in a predator, so that the fish can afford to broaden its ethmoid region without strengthening it with additional bone. It is the cartilage that is enlarged and in enlarging it appears to have separated the mesethmoid from the influence of the upper wings of

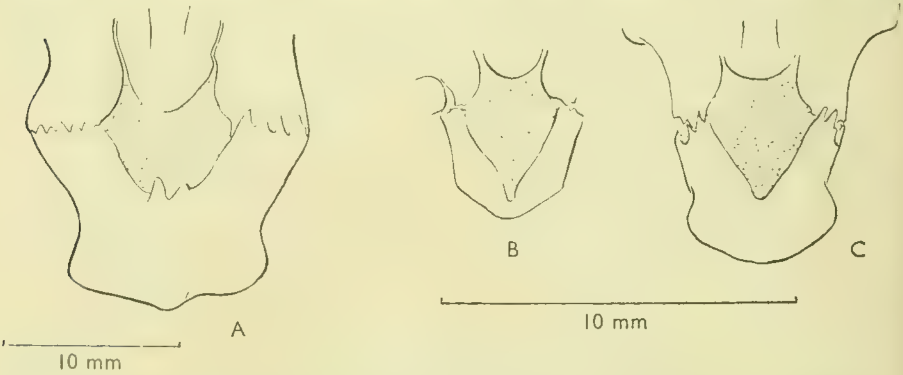

FIG. 14. Ethmovomerine region in *Sarotherodon* and *Stomatepia*. A, *Sarotherodon shiranus*, B, *Stomatepia mongo* and C, *St. pindu*. Cartilage dotted.

the vomer. A specimen of *Tilapia dageti* (fig. 13C) in which a tongue of the mesethmoid bone meets the vomer on one side gives a distinct impression of one bone influencing the other on the right side, whereas the rounded edge of the mesethmoid in *T. rendalli* (fig. 13B) and *Sarotherodon* (fig. 14A) looks like a bone developing freely from its own centre of ossification.

That the free ethmoid is not a necessary concomitant of a broad head is shown for instance by the South American *Cichlasoma bimaculata* (Linnaeus) a species with a very broad head in which the ethmoid cartilage is completely roofed by bone. Its dental equipment suggests that it feeds on bottom-living arthropods.

If the free ethmoid of *Sarotherodon* has arisen as a result of a functional response, it seems to have become genetically established so that the process is not reversible. So it is retained in the algal-grazing *S. alcalicus* and in the predatory *Stomatepia* of Barombi Mbo (fig. 14B and C), although the latter have developed narrow heads, strong jaws and short guts while showing affinity to *Sarotherodon* in the gill-raker numbers, pharyngeal bones and large, presumably mouth-brooded eggs (see Trewavas, Green and Corbet, 1972).

The following is a list of the species in which the ethmo-vomerine relationship has been examined, one specimen of each except where numbers follow the name. $\frac{1}{2}$ signifies meeting on one side but not the other; such specimens appear in both lists. In addition, in one *T. dageti* and two *T. discolor*, listed among those with a free ethmoid, the ethmoid sends out a short tongue on one side that fails to meet the vomer. To both lists are added the species of Barombi Mbo believed to be derivatives respectively of *Tilapia* and *Sarotherodon*.

Mesethmoid meeting vomer

Tilapia sparrmanii A. Smith (3)
T. busumana (Günther)
T. dageti Thys van den Audenaerde ($1\frac{1}{2}$)
T. guineensis (Bleeker) ($\frac{1}{2}$)
T. joka Thys van den Audenaerde
T. mariae Boulenger
T. guinasana Trewavas
T. zillii Gervais (9)
T. kottae Lönnberg
T.(?)*camerunensis* Lönnberg
Pungu maclareni (Trewavas) (2)
Tristramella simonis (Günther)

Mesethmoid free from vomer

Tilapia rendalli Boulenger (3)
T. zillii Gervais (1)
T. guineensis (Bleeker) ($\frac{1}{2}$)
S. galilaeus (Linnaeus)
S. niloticus (Linnaeus)
S. linnellii (Lönnberg)
S. lohbergeri (Holly)
S. spilurus (Günther)
S. amphimelas (Hilgendorf)
S. hunteri (Günther)
Stomatepia mariae (Holly)
Stomatepia mongo Trewavas
Konia eisentrauti (Trewavas)
T. dageti Thys ($3\frac{1}{2}$)
T. discolor (Günther) (2)
Sarotherodon melanotheron Rüppell (2)
S. aureus (Steindachner)
S. caroli (Holly)
S. steinbachi (Trewavas)
S. percivali (Boulenger)
S. shiranus (Boulenger)
S. alcalicus grahami (Boulenger)

Stomatepia pindu Trewavas
Myaka myaka Trewavas (2)
Konia dikume Trewavas

The reproductive and parental behaviour patterns divide the genera quite sharply, in spite of much evidence that the mouth-brooders have descended from substrate-spawners; and the two patterns carry with them contrasting structural and developmental features that have been admirably analysed for the species known to them by Baerends & Baerends van Roon (1950), Lowe (1959), Peters (1961), Kraft & Peters (1963), Peters (1965), Fishelson (1966), Heinrich (1967) and others. On the one hand the mouth-brooders exhibit certain vestigial features that can only be interpreted as evidence of substrate-spawning ancestry -vestigial adhesive organs in the embryo, sparse adhesive threads on the egg surface in *S. galilaeus* and *S. melanotheron*. On the other hand certain parallel developments with *Sarotherodon* occur within *Tilapia*, of which the freedom of the ethmoid from the vomer in *T. rendalli*, though not connected with reproduction, is perhaps the most indicative of the close phyletic relationship of *Tilapia* with *Sarotherodon*. Without this the question might remain open as to whether the substrate-spawning ancestors of *Sarotherodon* were indeed *Tilapia* and not some other genus from which *Tilapia* and *Sarotherodon* might independently have developed the structural adaptations to a herbivorous diet.

Irvine & Trewavas (in Irvine, 1947) and Thys (1970) have suggested, from the presence of eggs or young in the mouths of 4 of a total of 23 mature males of *Tilapia discolor* examined, that a primitive mouth brooding may be practised by this species. Examination of two of these eggs by the electron scanning microscope showed the presence of sparse filaments on the surface, resembling those of *Sarotherodon galilaeus* rather than the dense filaments of *T. tholloni* figured by Kraft & Peters (1963). Before this is classified as parallelism with *Sarotherodon* more evidence is needed, even to prove that they were the eggs of the same species. Their size-range (long diam. 2·6 3·2 mm) reaches that of known mouth-brooded eggs of *S. multifasciatus* (3·2 mm) of the same locality, Lake Bosumtwi. It need not be surprising to find mouth-brooding independently developed in *Tilapia* and *Sarotherodon*. The species of *Tristramella*, closely related to *Tilapia*, are mouth-brooders (Ben-Tuvia, 1959) as well as others not so close.

A similar report by Pellegrin (1907a and b) concerning a '*Tilapia melanopleura*' of the Ogowe system with larvae in the mouth has generally been ascribed to the habit, well known in species of *Tilapia* (as well as other cichlid substrate-spawners) of transporting embryos from one pit to another. This is less likely to be the explanation in the case of *T. discolor*, not only on account of the structure of the egg surface, but because the transpo tation usually occurs after hatching, when the adhesive egg-shells remain attached to the substratum.

Chardon & Vanderwalle (1971), in a study of the head of *T. discolor* and two other species of *Tilapia* and two of *Sarotherodon*, found that *T. discolor* shared with the other two *Tilapia* species certain differences from the two *Sarotherodon* and that such specific (or individual?) differences as he found between the *Tilapia* species had no bearing on the function of mouth-brooding.

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II A NEW SPECIES OF CICHLID FISHES OF RIVERS QUANZA AND BENGO, ANGOLA, WITH A LIST OF THE KNOWN CICHLIDAE OF THESE RIVERS AND A NOTE ON *PSEUDOCRENILABRUS NATALENSIS* FOWLER

By ETHELWYNN TREWAVAS

ABSTRACT

A species of the tilapiine genus *Sarotherodon*, formerly confused with other species, is described. An annotated list of the cichlid species of Rivers Bengo and Quanza is added, from which it appears that the cichlid fauna of the Bengo and Lower Quanza is related to that of the Chiloango and Ogowe, but that of the Upper Quanza to the Zambezi basin and R. Cunene, southern Angola.

The holotype of *Pseudocrenilabrus natalensis* is a specimen of *Chromis philander* Weber. Reasons are given for agreeing with Wickler that it is related to *Chromis multicolor* Hilgendorf and that both are generically distinct from *Haplochromis*. *Pseudocrenilabrus* is their earliest valid generic name.

Good samples of the species about to be described have been in the British Museum (Natural history) since 1910 as part of the collections of Dr W. S. Ansorge, but were not recognised as distinct from *Tilapia flavomarginata* Boulenger (= *S. schwebischi* (Sauvage)) and *S. andersonii* (Castelnau), species with respectively a more northern and more southern distribution. Parts of Ansorge's collections of this species were sent to the Academy of Sciences, Philadelphia, and to the Vienna Museum, where they were also catalogued under the names *T. andersonii* and *T. flavomarginata*. A still earlier collection had been made by the American Eclipse Expedition of 1889, and in his report on this collection Fowler (1919) recorded this species as *T. andersonii*.

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The generic assignment

I use the name *Sarotherodon* Rüppell, formerly recognised as a subgenus of *Tilapia*, at generic level for reasons given on p. 20 above.

Sarotherodon angolensis sp. n.

Plate 1

Tilapia flavomarginata (partim, nec Boulenger 1899); Boulenger, 1910 : 560 (Rivers Quanza and Bengo).

Tilapia andersonii (partim, nec Castelnau); Boulenger, 1911 : 415 (part of syn. *flavomarginata* only); id. 1915 : 171 (nos 26–38 only); Fowler, 1919 : 248 (R. Quanza at Cunga); id. 1931 : 81 (R. Quanza at Cambambe).

Tilapia (*Loruwiala*) *angolensis* Trewavas in Thys van den Audenaerde, 1968 : xxxvi (*nomen nudum*).

Local name: cacusso.

Holotype: ♂ of SL 196 mm from R. Quanza at Cambambe, coll. W. J. Ansorge. BMNH 1911.6.1.140.

Paratypes: 27 specimens comprising 12 ♂♂, 6♀♀ and 9 juveniles, of SL 43–204 mm from the lower Quanza at Cambambe and Cunga, collected by W. J. Ansorge in 1910 and W. H. Brown in 1899. These are in the collections of the BMNH the Vienna Museum, the Philadelphia Academy of Natural Sciences (all collected by Dr Ansorge) and in the U.S. National Museum (collected by W. H. Brown). See p. 27.

Natural distribution. Known from the lower reaches of the Quanza and Bengo only. In R. Quanza there are no verified records from above the cataracts of Cabulo, at Cambambe, about 6–8 miles above Dondo.

Distinguishing characters. A *Sarotherodon* with high numbers of gill-rakers, 21–26 on the lower part of the anterior arch; a lower pharyngeal bone with slender crowded teeth and a long anterior blade; a tasselled genital papilla in both sexes, longer in the male. Distinguished from other such *Sarotherodon* species by the colour pattern of mature individuals, in which the vertical fins *and the pelvics* bear small round white spots; in males in addition each scale of 8–11 longitudinal rows bears a bright silver spot (colour in alcohol). There is sexual dimorphism also in the teeth, the outer lateral of both jaws becoming unicuspid and slightly enlarged in mature males.

Description of the holotype and paratypes and of two specimens from the lower Bengo at Cabiri and three from Lake Panguila near the mouth of R. Bengo, in all 32 specimens of SL 43–204 mm.

Proportions as % SL

Depth of body 38·0–44·0.
Length of head 33·3–36·0.
Length of pectoral fin 37·5–44·0 (35 at SL 43–46 mm.)
Length of last dorsal spine 16·0–20·0 (14 at SL 43 mm).
Length of third anal spine 13·0–17·5.
Length of caudal peduncle 12·5–15·3 (0·8–1·0 of its depth).

Proportions as % length of head

Length of snout 31·0–35·5 (30 at SL 43 mm).
Diameter of eye 20–26 at SL 90–204 mm, negatively allometric; 27–30% at SL 83 and 43 mm.

Depth of preorbital 18–22 with very little allomtery with the head length at SL 100–204 mm, approximately equal to eye between 140 and 204 mm.
Interorbital width 37–40·5 at 100–200 mm SL, 33–36·5 below this length.
Length of lower jaw 29·3–34·0, with no difference correlated with age or sex.
Width of mouth 27–34.

Profile of snout descending in a straight line. Dorsal and anal fins with bases ending at the same vertical or anal a little more posteriorly (in contrast to most species, in which if either fin is posterior it is the dorsal).

Teeth of jaws in 4–6 series at SL above 140 mm, 3–4(5) below this length; 60–92 in outer series of upper jaw at SL 100 mm or more, often fewer below this length; outer bicuspid in females and young, but in mature males the lateral teeth in both jaws become unicuspid and a little enlarged and spaced; inner teeth tricuspid. The bicuspid teeth have slender shafts, spoon-shaped major cusps and small minor ones.

Gill-rakers on first arch (2–5) + 1 + (21–26). Microbranchiospines present on the outer sides of 2nd, 3rd and 4th arches.

Length of lower pharyngeal bone 37–40% of length of head, width 28·5–31%; teeth very fine and densely crowded, the toothed area with broad rounded lateral lobes and a short narrow apex; blade 1·3 to nearly twice the median length of the toothed area.

Vertebrae 29 (in 3 specimens).

Scales on cheek in 2–3 series; in lateral line series 29 (f. 1½), 30 (f.19), 31 (f.7½), or 32 (f.1); between origin of dorsal and lateral line 3½ (f.1), 4 (f.20), 4½ (f.7) or 5 (1); between bases of pectoral and pelvic fins 4–5, moderately small on chest but not very small on belly.

Dorsal XV 12, XVI 11–12 or XVII 11; modal combination XV12 (in 15 of 33 specimens). Total rays 27 (f.26) or 28 (f.7).

Anal III 8 (f.1), III 9 (f.12) or III 10 (f.15).

Pelvic produced to a short filament, in mature fish reaching anal spine. Caudal slightly emarginate.

Genital papilla in immature male bluntly bifid, in mature male with lobes, filaments and tubercles in two bunches, about 1 cm long. Posterior border of female papilla also tuberculate, but not as long as in male.

Colour in alcohol shading from light brown above to white on the belly. In mature ♂ each scale of 8–11 longitudinal rows below the upper lateral line with a bright silvery spot. In both sexes in mature and maturing fishes conspicuous small round white spots appear on the dorsal, caudal and anal fins and on the pelvics; on the caudal also some dark spots. Male with white lower lip and narrow white (red in life?) upper edge of soft dorsal fin.

Bionomics. No data. Other species with tasselled genital papilla are maternal mouth-brooders. Near-ripe ovarian eggs in one specimen measure 3 mm in long diameter.

AFFINITIES. Thys (1968: xxxvi) in publishing this name and attributing it to me, placed it in his subgenus *Loruwiala* (type *S. macrochir* Boulenger), characterised by the presence of a genital tassel in the male. This is the only character by which he distinguished *Loruwiala* from subgen. *Nyasalapia* Thys (op. cit. p. xxxv) whose type species, *S. squamipinnis* (Günther), and all others listed also have a genital tassel in the male and are I believe closely related to *S. macrochir*. I would consider *Loruwiala* and *Nyasalapia* to be subjective synonyms and propose to use the latter as the valid name.

Whether the genital tassel is a sufficient sign of close relationship I am not quite sure. In the case of *S. macrochir*, *S. rukwaensis* (Hilgendorf) and the species-group of *S. squamipinnis* we have other evidence of interrelationship, but *S. upembae* Thys and *S. variabilis* Boulenger are more remote both structurally and geographically. As I show below, the cichlid fauna of the lower Quanza and Bengo lacks certain widespread species of the upper Zambezi and Upper Zaire and has two species of *Tilapia* in common with the Chiloango and Ogowe. The *Sarotherodon* of these rivers is *S. schwebischi*, but although Thys puts it in *Loruwiala* I have seen no specimen with a genital tassel. *S. lepidura* Boulenger of the Lower Zaire (Congo) is a tasselled species, but otherwise shows no special resemblance to *S. angolensis*. There seems nothing better to do than to place *S. angolensis* with the tasselled Sarotherodons while admitting that it is such a distinctive species that it throws some doubt on the presence of a tassel as a necessary indicator of relationship.

MATERIAL EXAMINED

Museum & reg. no.	SL (mm)	Locality	Collector
Vienna Museum 24679–83 paratypes	2 ♂♂ 169, 204 3 imm. 87·5–106	R. Quanza at Cambambe	W. J. Ansorge
BMNH 1911.6.1 140–142 holotype & paratypes	♂196, 2 ♀♀ 138, 198	,,	,,
BMNH 1911.6.1 143–147 paratypes	43–177 (2 ♂♂, 1 ♀, 2 imm.)	R. Quanza at Cunga	,,
USNM 42323/327	148	,,	W. H. Brown Eclipse Expedn.
42324/328–9	141, 157·5		
42325/330–335 paratypes	125·5–150·5		
Philadelphia Academy 37976–81 paratypes	46·5–155	R. Quanza at Cambambe	W. J. Ansorge
BMNH 1911.6.1 138–9	191, 195	R. Bengo at Cabiri	,,
BMNH 1911.6.1 148–150	90–130	Lake Panguila R. Bengo	,,

CICHLIDAE OF RIVERS BENGO AND QUANZA

Cichlidae have been collected in R. Bengo from Lake Panguila near the coast and Lake Rumanga at Cabiri. In the Quanza system they were taken at Cunga and Cambambe, both localities downstream of the rapids at Cabulo, and also from 'R. Luculla' (=Lucala), a tributary entering the lower Quanza from the North. In addition the Gray African Expedition collected at Chouzo on the Upper Quanza (ca. 11°48′S 17°30′E) and in the Luce River, a tributary of the Upper Quanza, and these fishes were reported on by Fowler (1931; Cichlidae pp 44–46). I have examined the Gray Expedition's fishes and find that Fowler's determinations as *T. cabrae* and *T. lucullae* were both mistaken. The determinations by Gianferrari (1932) of three cichlid species from the "alto corso dei Quanza" are, even on her own evidence, mistaken. Dr Cagnolaro of the Milan Museum informs me that the collections of the Baragiola-Durini expedition, on which her report was based, were destroyed during the second world war, so I omit her records.

R. Bengo

Tilapia cabrae Boulenger, 1899a: 51 pl. xxvii (type locality Chiloango). Synonyms *T. haugi* Pellegrin, 1912: 274 pl. i (Ogowe) and *T. ngomoensis* Pellegrin, 1913 : 274 (Ogowe).

Reported from R. Bengo by Boulenger, 1915 : 194, and Fowler, 1931 : 46.

The Angolan samples have a somewhat coarser pharyngeal dentition than those from the Ogowe and Chiloango and in them the dorsal spines number XIV–XVI, mode XV, as against XVI–XVII, mode XVI, in those from the localities North of the Zaire (Congo).

Sarotherodon angolensis (see above).

R. Lucala

Haplochromis lucullae (Boulenger, 1913 : 483; 1915 : 224 fig. 146). Recorded from this river, the type locality, by Boulenger (l.c.) and by Fowler (1931 : 44). Regan (1922) synonymized it with *H. acuticeps* (Steindachner), but the types of this species, which I have seen, have some of the pharyngeal teeth enlarged and blunt while those of *H. lucullae* are all slender and pointed. *H. acuticeps* has 32–33 scales in the lateral line series, *H. lucullae* only 31. *H. lucullae* seems to be closely related to *H. schwetzi* Poll, 1967, of R. Kwango, Angolan Zaire (Congo) system.

H. multiocellatus (Boulenger, 1913 : 484; 1915 : 409 fig. 278). The holotype, a specimen of 98 + 24 mm, resembles *H. acuticeps* (Steindachner) in having some enlarged teeth in the pharynx and 33 scales in the lateral line series. The outer teeth of the jaws are all unicuspid, but a few have a minor cusp represented by a shoulder. In the types of *H. acuticeps*, all of which are smaller, the outer teeth are bicuspid, but the difference may be a matter of age. Both have only one row of inner teeth, though *H. multiocellatus* has a few of a second row in the lower jaw, and in this they differ from *H. thysi* Poll, 1967, of R. Kasai system. The locality of *H. acuticeps* was given no more precisely than "Angola" and I am inclined to think that *H. multiocellatus* is its synonym. The one specimen from R. Lucala retained by Boulenger (1915 : 218) as *acuticeps* is a young *H. lucullae*.

Lower Quanza

Hemichromis fasciatus Peters, 1858. A widespread species. Coll. Ansorge at Cunga, and reported by Boulenger (1910, 1915).

Tilapia guineensis (Bleeker in Günther, 1862 : 271). Type locality Ghana (Gold Coast). Two specimens in the BMNH were collected by Ansorge at Cunga in 1910 and recorded as *T. melanopleura* by Boulenger (1910 and 1915) and eight were taken by W. H. Brown of the American Exlipse Expedition, also at Cunga, and recorded by Fowler as *T. andersonii*. I determine these now as *T. guineensis* rather than any other species because of the shape and size of the lower pharyngeal bone, which contrasts with the stouter bone of *T. rendalli* Boulenger, the species inhabiting the inland waters of Angola and the Zambezi system. The bone is, however, a little heavier than that of the populations of the lagoons bordering the Gulf of Guinea and the fins, which are damaged, do not seem to have been as long as they characteristically are in the region of the type-locality.

Tilapia cabrae Boulenger. Specimens in the BMNH, the Philadelphia Academy of Sciences and the U.S. National Museum from Cunga and Cambambe.

Sarotherodon angolensis

UPPER QUANZA AT CHOUZO

Pseudocrenilabrus philander (Weber, 1897).

Two specimens recorded as *T. cabrae* by Fowler (1931 : 46) and 17 recorded by Fowler (t.c. p. 44) as *T. lucullae* prove to be referable to this species, which is widespread in the upper tributaries of the Zaire (Congo), throughout the Zambezi system, in the Lake Malawi basin (but not in the lake), Lake Chilwa, the Limpopo system and he rivers of Natal and Zululand, R. Cunene, R. Okovango (Cubango) and the sink-holes of Southwest Africa (see also next page).

Tilapia sparrmanii A. Smith, 1840.

The Gray African Expedition brought 151 specimens of this species from Chouzo. It has almost the same distribution as *P. philander* and the two species are commonly found together. Only in the sink-holes of Southwest Africa (Lakes Guinas and Otjikoto) is it replaced by *T. guinasana*. All the Angolan localities recorded by Poll (1967) are on the Cassai and Cuango of the Zaire (Congo) system and on the upper Zambezi. Boulenger (1915 : 207) listed examples from the Cunene system (R.Que) and Fluilla (probably = Huila, Mossamedes).

Tilapia rendalli Boulenger.

Two specimens in the Philadelphia Academy collected by the Gray Expedition.

These three species (*P. philander*, *T. sparrmanii* and *T. rendalli*) were mistakenly listed by Fowler as "a large series of over 100 examples" of *T. cabrae*.

Serranochromis macrocephalus (Boulenger 1899b).

13 specimens collected by the Gray African Expedition are in the Philadelphia Academy and were recorded by Fowler (1931 : 44) as "*Tilapia acuticeps* (Steindachner)". They measure 106–170 mm in SL and have a dorsal formula of XIV–XV 12–14. This species also has a wide distribution in southern Africa, from the Cunene system, the Cubango and Okovango, Upper Zambezi and Kafue to Lake Mweru (see Trewavas, 1964 : 29–33).

LUCE RIVER, entering Upper Quanza at about 10°15'S 16°35'E.

Pseudocrenilabrus philander (Weber, 1897), recorded by Fowler (1931) as *Tilapia lucullae* Blgr.

Ladiges (1964) divided Angola into five zoogeographical provinces:

(1) Angola Province—rivers north and west of the watersheds
(2) Kasai (Cassai) district
(3) Cunene system
(4) Ngami basin with Okovango-Cubango
(5) Zambezi basin

As far as the cichlids are concerned, provinces (3–5) may be bracketed together. The Bengo and Lower Quanza belong to Province (1), but the Upper Quanza is evidently part of (3–5). Marquardson (1920 : 39) refers to the interdigitating of the sources of the Quanza and Cubango. The courses of the Quanza and its tributaries are punctuated by falls and rapids until finally at Cambambe the Cabulo cascades mark the upper limit of navigability. Whether the division between the two faunae is at the same point can be known only after further ichthyological exploration.

Ladiges (1964) and Poll (1967) remark on the high degree of endemicity in the fish fauna of the Angolan Province. The recognition of *Sarotherodon angolensis* and the differences between the Angolan populations of *Tilapia cabrae* and those of more northern rivers reinforce this observation.

THE IDENTITY OF *PSEUDOCRENILABRUS NATALENSIS* FOWLER

Fowler, 1934 : 462, 463, fig. 36.

When I was visiting the Philadelphia Academy of Sciences in 1963 Dr J. Böhlke told me that he believed the holotype of this nominal species to be a cichlid. I examined it and found it to be a specimen of *Chromis philander* Weber, 1897, usually known as *Haplochromis philander*. Dr Jubb, to whom I communicated this opinion, has commented on its implication (1971) and his comments will be considered below.

The type (ANSP no. 55175) is a ♀ of 59+17 mm collected by Mr H. W. Bell-Marley near Durban, 1929–32.

Proportions as % SL: depth 33·8, length of head 37·2, length of pectoral fin 26·2, of caudal peduncle 14·6 (1·2 times its depth).

Proportions as % length of head: diameter of eye 29·0, depth of preorbital 15·5, interorbital width 21·0, length of lower jaw 45·4, of premaxillary pedicels 34·1.

Teeth in 5 series, the outer all bicuspid (*pace* Fowler), although the minor cusp is very small; inner tricuspid; 44 in outer series of upper jaw.

Gill-rakers on first arch 3 + 1 + 8, triangular or square in shape. Pharyngeal teeth compressed, pointed, each with a major and a minor cusp or shoulder, a pair of middle posterior a little stouter than the rest.

Scales on cheek in 3 series, in lateral line series 29.

Dorsal XV 10. Anal III 9.

In comparing this with other samples of *Ps. philander* the size of the jaw is striking. Although since I proposed to recognize three subspecies (Trewavas, 1936), more variation has been found in the mouth-size of the populations then named *Ps. philander* *dispersus*, the biggest mouths are still those of the southeastern samples belonging to the nominate subspecies.

Generic assignment

Although *Chromis philander* has long been included in *Haplochromis*, Wickler (1963) has proposed to transfer it to *Hemihaplochromis* Wickler, 1963, of which *H. multicolor* Hilgendorf is the type species. If these two species are held to constitute a distinct genus its name must be the earlier *Pseudocrenilabrus*.

This involves two decisions—(1) to recognize intrageneric relationship between *multicolor* and *philander* and (2) to distinguish both of them generically from *Haplochromis*.

Haplochromis as at present constituted includes over 150 species in Lake Victoria because of their evident close inter-relationship as a flock that includes *H. obliquidens*, the type species. *H. obliquidens* is not the most generalized of this flock, but among the more generalized members of it are some with obvious affinity to the *Haplochromis* of the rivers of Tanzania and Uganda, including *H. pectoralis* Pfeffer, type species of *Ctenochromis* Pfeffer, which is therefore considered a synonym of the earlier name *Haplochromis*.

Within their endless diversity the species of *Haplochromis* have almost universally in common a feature of the colour-pattern, the well-known ocellar spots on the anal fin of the male. In some species these may be present in the female too. Dr R. Welcomme showed me some ripe female *H. nubilus* with well-developed orange anal ocelli and I have seen ripe females of *H. bloyeti* as well as males with the same.

Such yellow, orange or orange-red spots are so characteristic of *Haplochromis* that as mere structures (and quite apart from their function) they are impressive indicators of relationships. *Ps. multicolor* and *Ps. philander* have no such spots, but instead have an orange* or scarlet tip to the anal fin. This is not, to human eyes, a very conspicuous spot and in *philander* is neither the same colour nor the same size as the eggs.

Wickler (1962 a & b) has shown that the ocellar spots of male *Haplochromis* are treated by the female exactly as if they were her newly laid eggs. No one who has seen Wickler's film of *H. burtoni* can doubt that the female has indeed mistaken them for eggs and is trying to pick them up to add to the clutch already in her mouth. In so doing she takes the sperm-laden water around the male's genital papilla and doubly ensures the fertilization of the eggs in her mouth. For this reason Wickler calls the spots "eggdummies" or "egg-spots", but his objection (1962) that they should not be called ocellar spots because their function is not to be mistaken foreyes is not valid. This epithet is simply descriptive of spots (in many animals) that to us resemble eyes because they are ringed, and we continue to use it as a descriptive term.

The male *Haplochromis* reinforces this deception by spreading his anal fin in front of the female.

---

* Orange in *multicolor* according to Wickler, but bright red according to Sterba (1959 and 1962).

In *Ps. multicolor* also the female mouths the water near the male's genital papilla and anal fin. But the male extends his anal fin without spreading it (Wickler, 1963 : 91; Zukal, 1971 : 10). According to Wickler he opens it just enough to make the orange tip of the fin the same size as the eggs! In *Ps. philander* the scarlet tip is surely too small to be taken for an egg. In Ribbink's account (1971) of the spawning of this species (probably the Natal population) he states that both dorsal and anal have black leading and orange trailing edges. No apical spot is mentioned and far from showing interest in the tip of the fin the female appeared to be guided by the concave spread of the fin and its series of dark spots to snap up sperm close to the male's genital papilla.

The basic fact is that in several (perhaps all) mouth-brooding cichlids that pick up the eggs immediately after they are laid the female snaps at the sperm-laden water near the male's papilla as soon as she has the eggs in her mouth. In some, perhaps all, these species movements of the male's anal fin provide a visual attraction and perhaps limit the dispersal of the sperm. In certain groups—*Haplochromis*, the tasselled *Sarotherodon*, species with a white or yellow genital papilla, *Ps. multicolor* but perhaps not *Ps. philander*—different devices have evolved reinforcing this action by using the peak of the female's urge to pick up the egg to deceive her into active drawing of the sperm into the mouth.

It is the fact that the same end has been achieved by the use of different colour-markings in *Haplochromis* and *Pseudocrenilabrus* that is the main justification for our use of the generic division. Supporting reasons are more difficult to define. Not only the anal fin but the whole colour scheme of the genera is in contrast. It has been described in the publications of Greenwood (*Haplochromis*) and in the aquarium literature (*Pseudocrenilabrus*) and is well illustrated in the black-and-white figures 1 and 2 of Wickler (1963). The caudal fin is well rounded in *Pseudocrenilabrus*, usually truncate or truncate with rounded corners in *Haplochromis* (emarginate in Malawi species, but these constitute a distinct group).

Both species of *Pseudocrenilabrus* have 28 vertebrae and, like *Haplochromis*, a well-marked facet for the upper pharyngeals in which parasphenoid and basioccipital contribute approximately equal parts.

Structural differences between *Ps. multicolor* and *Ps. philander* are especially the wider interorbital region and smaller mouth of *Ps. multicolor*.

Both species have wide but complementary distributions. *Ps. multicolor* in the Nile, in the streams and swamps of Uganda, round the shores of Lake Victoria and (personal comm. P. H. Greenwood) the shallow, reed-fringed Kazinga Channel between Lakes Edward and George and occasionally at the shore of Lake George. *Ps. philander* is a species of backwaters, swamps and shallow lagoons in the Zambezi, Limpopo and upper Zaire (Congo) basins, in the river-systems of Natal and Zululand, the Orange River* basin and in the sink-holes of Southwest Africa. In their respective areas they have no close relations, they do not live a truly lacustrine life nor give rise to species flocks. Where in the Lake Malawi basin *Ps. philander* is found in lagoons together with *Haplochromis callipterus*, the *Haplochromis* enters the lake and lives around its shores, but the *Pseudocrenilabrus* will not.

---

* *Ps. philander* and *Tilapia sparrmanii* live together here (Jubb & Farquarson, 1961 : 119) including the Kuruman area, the type locality of *Chromys moffattii* Castelnau, which I dismissed as a *species dubia* in 1936 because the size given was much greater than that of any known *Ps. philander*. This is still true

Neither *Ps. multicolor* nor *Ps. philander* has been found in the Lake Tanganyika basin nor in the Middle or Lower Zaire (Congo), in the lower reaches of any Western rivers North of the Cunene nor in any part of the East African eastern drainage north of the Zambezi (if Lake Chilwa be excepted with its tenuous connection with the Rovuma via Lake Chiuta).

I sympathise with Dr Jubb's reluctance (1971) to use a cumbersome and rather inappropriate name for this pretty little *philander*, but it must share with the wren the burden of the rules of nomenclature.

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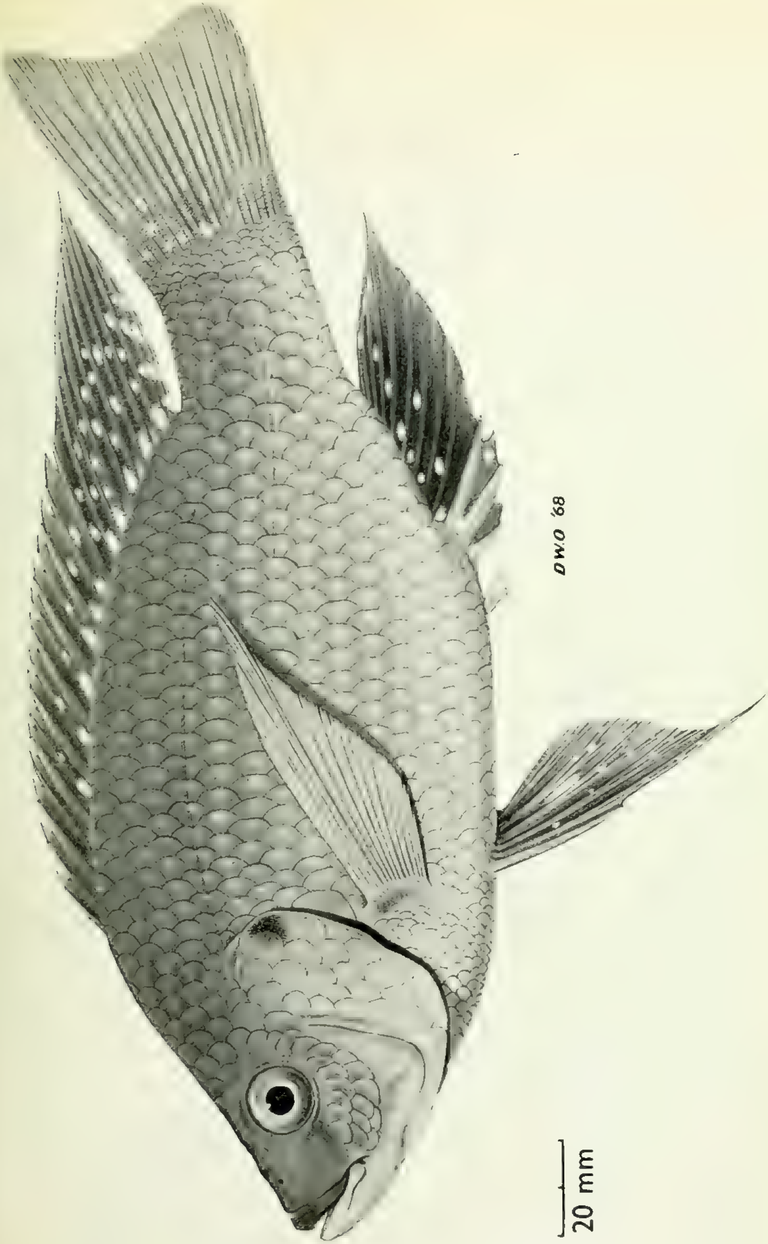
Sarotherodon angolensis, holotype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BY
E. H. EASON
Bourton Far Hill, Moreton-in-Marsh, Gloucestershire

Pp 39–83; 58 *Text-figures*

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By E. H. EASON

INTRODUCTION

Of the twenty nominal species described by Pocock in the genus *Lithobius*, eight belong to the Biologia Centrali-Americana Collection presented to the British Museum (Natural History) by Messrs F. D. Godman and O. Salvin. These are all fairly easily recognizable from their original descriptions and illustrations: although few have been redescribed they have all been referred by Chamberlin not only to genera other than *Lithobius* but to a family distinct from the Lithobiidae, the Gosobiidae. The remaining twelve species were described more scantily with or without indifferent illustrations: several have been redescribed and nearly all of them have been referred by Attems or Chamberlin to genera other than *Lithobius* within the family Lithobiidae.

The descriptions which follow are based on Pocock's original material which is preserved in spirit in the British Museum (Natural History). Study of these specimens inevitably raises the question of the validity of the family Gosobiidae and of the numerous genera and subgenera in which Pocock's species have, from time to time, been placed. To use the generic names applied to each species by Attems or Chamberlin would imply recognition of the genus in question, whereas to use them for some species and not others would require explanation quite beyond the scope of this paper. Each species is, therefore, placed in *Lithobius*: but a brief explanation of the use of other generic names is given in each case.

A complete synonymy is given for each of the valid species. For those which are shown to be junior synonyms, only the names applied to them by Attems or Chamberlin before their identity was recognized are cited.

Conclusions as to the validity and status of each species are summarized in Table 1.

Finally, two specimens from India among the syntypes of *L. sculpturatus* belong to a new species which is described·

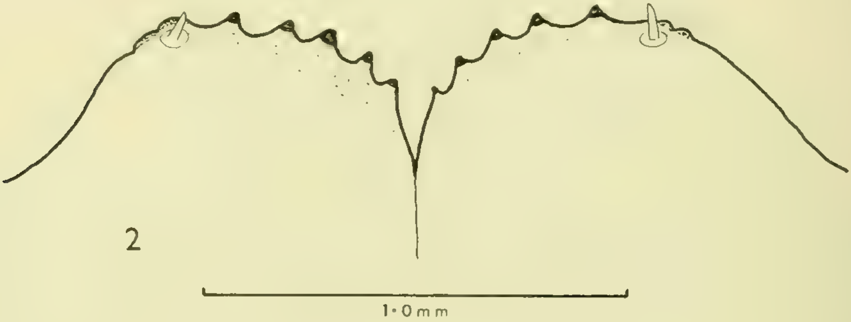
Note on the illustrations

Throughout this study, for clarity, the setae have been omitted from all the illustrations except those of the legs on which the setation may be of taxonomic importance.

1. *Lithobius macroceros* Pocock

(Figs. 1 to 3)

Lithobius macroceros Pocock, 1895a : 4, Tab. 1 figs. 3, 3a–d.
Sotimpius macroceros : Chamberlin, 1912 : 177.
? *Sotimpius multigranosus* Kraus, 1954 : 304, Taf. 28 figs. 20–23.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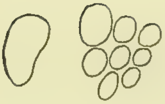
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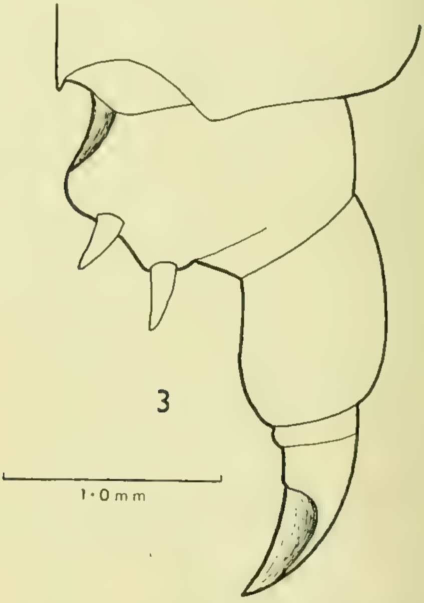
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FIGS. 1–3. *Lithobius macroceros*. Fig. 1. Ocelli. Fig. 2. Dental margin of prosternum, ventral. Fig. 3. Left ♀ gonopod, ventral.

Type locality. Omilteme, Guerrero, Mexico.

Material examined. A jar labelled "*Lithobius macroceros* Pocock, type, 1897.3.1.12–14" contains the following three tubes:

"Omilteme 811". A fairly well-preserved female (Reg. no. 1897.3.1.12).

"Omilteme 818". A mutilated female with the gonopods separated (Reg. no. 1897.3.1.13).

"Omilteme 820". A mutilated female pierced longitudinally by a pin (Reg. no. 1897.3.1.14).

Type specimen. The best preserved specimen, a female 35 mm long, is here formally designated as the lectotype (Reg. no. 1897.3.1.12).

Description. *Size*: 34 to 37 mm long and about 3·2 mm broad at T.10. *Colour*: dark brown. *Shape*: slender, almost parallel-sided; T.1 about as broad as T.3; body broadest at T.10. *Head*: broader than long, as broad as T.10 or broader. *Antennae*: over half body-length, of 59 irregular articles. *Ocelli*: 1 + 3, 3, 2 (Fig. 1). *Prosternum*: with 5 + 5 or 5 + 6 teeth; lateral spine much less stout than teeth at its base, probably pointed at apex in undamaged specimens, placed as far posterolateral to the lateral tooth as the interval between the two outermost teeth; on each side, adjacent to the insertion of the spine, are one or two feeble projections easily mistaken for teeth on casual examination; lateral to these projections the anterior border slopes gradually backwards without angulation; median cleft incised (Fig. 2). *Tergites*: posterior angles of T.8 rounded or blunt, those of T.10 blunt or angulated, those of T.12 angulated, those of T.14 angulated and sometimes slightly projecting; posterior emargination of large tergites very feeble or absent; large tergites unusually long for *Lithobius*, longer than broad (see Pocock 1895a: Tab. 1 fig. 3a); posterior angles of T.7 with feeble broad projections, those of T.9, 11 and 13 with narrower and more pronounced projections; intermediate tergite feebly emarginate posteriorly. *Coxal pores*: 6, 6, 6, 6; oblong. *15th leg*: barely exceeding one-third of body-length; accessory apical claw one-third of length of principal claw. *Female gonopod*: coxa markedly excavated medially at base, with two conical spurs separated from one another at their insertions by about twice their own breadth; claw simple (Fig. 3). *Male*: unknown.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	p	amp	am	—	—	mp	a	a
2	—	—	p	amp	am	—	—	mp	ap	a
3–4	—	—	(m)p	amp	am	—	—	mp	ap	a
5–6	—	—	mp	amp	am	—	—	mp	ap	ap
7	—	—	mp	amp	am	—	—	(a)mp	ap	ap
8–11	—	—	mp	amp	am	—	—	amp	ap	ap
12–13	(a)	m	amp	amp	am	—	—	amp	ap	ap
14	a	m	amp	amp	m	—	—	amp	ap	p
15	a	m	amp	amp	m	a	—	amp	—	—

Letters in brackets indicate variable spines.

REMARKS. Chamberlin (1912) noticed the medial excavation at the base of the coxa of the female gonopod (presumably in Pocock's illustration (Pocock 1895a: Tab. 1 fig. 3d) as there is no evidence of his having examined a specimen himself) and it was this feature which he used chiefly to characterize the Gosobiidae (Chamberlin 1917). *Sotimpius* (Chamberlin 1912), characterized by having numerous prosternal teeth, was erected to receive *L. macroceros* and *L. decodontus* Pocock, but both Pocock and Chamberlin (who merely copied Pocock) overstated the number of teeth by including the lateral spines.

Sotimpius multigranosus Kraus from El Salvador is so close to *L. macroceros*, from which it only differs in having rather shorter antennae, more marked posterior emargination of T.8, 10 and 12, and slightly different spinulation, that it may well prove to be conspecific.

2. ***Lithobius decodontus*** Pocock

(Figs. 4 and 5)

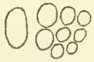
Lithobius decodontus Pocock, 1895a: 9, Tab. 1 figs. 9, 9a and b.
Sotimpius decodontus: Chamberlin, 1912: 177; 1921: 10; Kraus, 1954: 303.

TYPE LOCALITY. Volcan de Acatenango, Guatemala.

MATERIAL EXAMINED. A jar labelled "*Lithobius decodontus* Pocock, type, 1894.4.1.74" contains the following two tubes:
"Volcan de Acatenango, Stoll". A well-preserved male 17 mm long.
"Quezaltenango". A mutilated male.

TYPE SPECIMEN. Pocock made it quite clear that his description was based on a single male from Volcan de Acatenango and that he was uncertain of the identity of the one from Quezaltenango. The former is therefore the holotype (Reg. no. 1894.4.1.74 (part)).

DESCRIPTION. *Size*: 17 to 19 mm long and about 2·0 mm broad at T.10. *Colour*: brown. *Shape*: almost parallel-sided; T.1 about as broad as T.3; body broadest at T.10 which is barely broader than T.5 and 8. *Head*: barely broader than long, as broad as T.10. *Antennae*: almost half body-length, of 42 or 43 mostly transverse articles. *Ocelli*: 1 + 3, 3, 2 (Fig. 4). *Prosternum*: with 3 + 4 or 4 + 5 teeth; lateral spine less stout than teeth at its base, pointed at apex, placed posterolateral to lateral tooth; lateral to the spine the anterior border slopes gradually backwards without angulation (Fig. 5). *Tergites*: posterior angles of T.8 blunt, those of T.10 blunt or angulated, those of T.12 angulated and very slightly projecting, those of T.14 angulated and distinctly projecting; posterior borders of large tergites straight, not emarginate; large tergites rather long, as long as broad or longer but relatively shorter than in *L. macroceros*; posterior angles of T.7 with very feeble broad projections, those of T.9, 11 and 13 with narrower and more pronounced projections; intermediate tergite feebly emarginate posteriorly. *Coxal pores*: 5, 5, 5, 5 or 4, 5, 5, 4; circular; separated from one another by their own diameter. *15th leg*: almost half body-length, not swollen or otherwise modified; accessory apical claw one-third of length of principal claw. *Female*: unknown.



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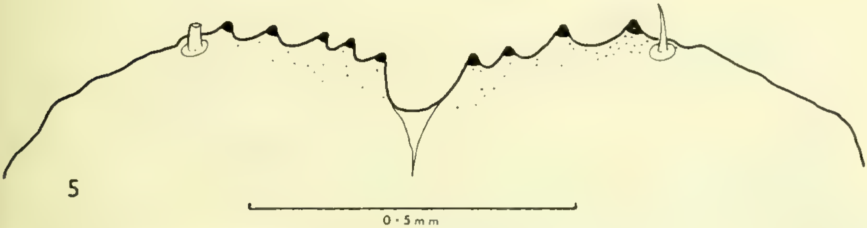

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FIGS. 4–5. *Lithobius decodontus*. Fig. 4. Ocelli. Fig. 5. Dental margin of prosternum, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1–2	—	—	—	am	am	—	—	mp	a	a
3–4	—	—	p	am	am	—	—	mp	ap	a
5	—	—	p	amp	am	—	—	mp	ap	a
6–7	—	—	mp	amp	am	—	—	mp	ap	ap
8	—	—	mp	amp	amp	—	—	mp	ap	ap
9–10	—	—	mp	amp	amp	—	—	amp	ap	ap
11	—	—	p	amp	amp	—	—	amp	ap	ap
12	—	—	amp	amp	amp	(a)	—	amp	ap	ap
13	(a)	m	amp	amp	amp	(a)	—	amp	ap	ap
14	a	m	amp	amp	amp	a	—	amp	ap	ap
15	a	m	amp	amp	am	a	—	amp	p	—

Letters in brackets indicate variable spines.

REMARKS. Chamberlin's (1912) inclusion of this species in *Sotimpius* must have been on the assumption that the coxae of the female gonopods are similar to those of *L. macroceros*, as the female of *decodontus* seems never to have been described. The two species, however, are certainly closely related and probably belong to the same species-group.

Pocock recorded 6 + 4 prosternal teeth for the holotype but must have counted the rather stout right lateral spine (Fig. 5) as a tooth. He was uncertain of the identity of the male from Quezaltenango owing to the metatarsi of the anterior legs being much shorter than the corresponding tarsi, and he believed it might belong to another species. But there is no difference between this specimen and the holotype in the relative lengths of these articles and there is no doubt that they both belong to the same species.

3. ***Lithobius godmani*** Pocock

(Figs. 6 to 11)

Lithobius godmani Pocock, 1895a : 6, Tab. 1 figs. 6, 6a–c.
Vulcanbius godmani : Chamberlin, 1944a : 201.

Type locality. Amula, Guerrero, Mexico.

Material examined. A jar labelled "*Lithobius godmani* Pocock, type, 1897.3.1.16–20" contains the following five tubes:

"*Lithobius godmani* Poc. type, Amula 1085". A fairly well-preserved male (Reg. no. 1897.3.1.16).

"*Lithobius oedipes* Pocock, Amula 1087". A rather mutilated male (Reg. no. 1897.3.1.17).

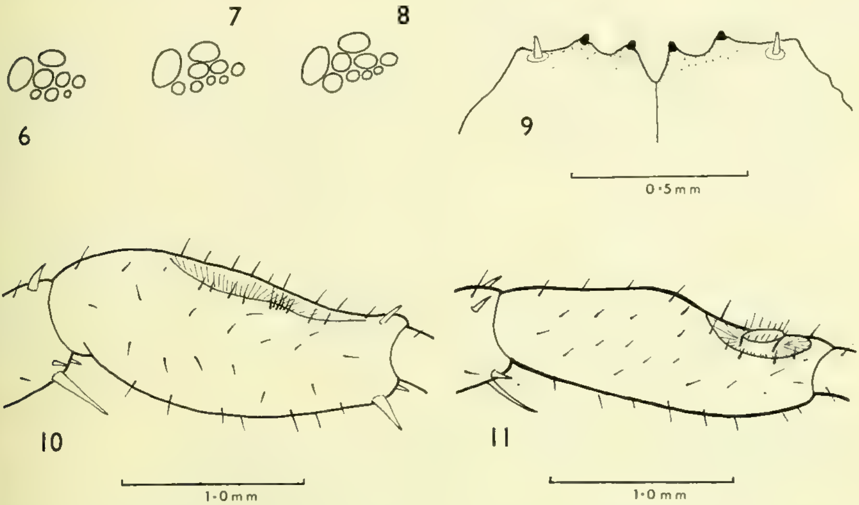
"Amula 1085". A mature male, an immature male and three immature females, all more or less mutilated (Reg. no. 1897.3.1.18).

"*Lithobius oedipes* Pocock, Amula 1086". Two males and two immature females, all in poor condition (Reg. no. 1897.3.1.19).

"1079 Amula". A very mutilated immature male (Reg. no. 1897.3.1.20).

Type specimen. The best preserved specimen, a male 18 mm long, is here formally designated as the lectotype (Reg. no. 1897.3.1.16).

Description. *Size*: 17 to 19 mm long and about 2·7 mm broad at T.8. *Colour*: brown. *Shape*: feebly fusiform; T.1 rather narrower than T.3; body broadest at T.8. *Head*: broader than long, as broad as T.1. *Antennae*: over half body-length, of 50 to 53 transverse to slightly elongate articles. *Ocelli*: 1 + 1, 3, 3 or 1 + 1, 3, 4 (Figs. 6, 7 and 8). *Prosternum*: with 2 + 2 teeth; lateral spine less stout than teeth at its base, probably setiform at apex in undamaged specimens, placed about as far lateral to the lateral tooth as the interval between lateral and medial teeth; lateral to the spine the anterior border forms a fairly sharp angle (Fig. 9). *Tergites*: posterior angles of T.8 angulated, those of T.10 sharply pointed, those of T.12 and 14 sharp and slightly projecting; posterior borders of large tergites straight or only feebly emarginate; posterior angles of T.7 with broad blunt projections, those of T.9 with broad angulated projections, those of T.11 and 13 with broad sharp projections, the internal borders of which are slightly sinuous; intermediate tergite straight posteriorly (in male). *Coxal pores*: 5, 4, 4, 4 or 5, 4, 4, 3; circular; separated from one another by their own diameter or less; specimens with 4, 3, 3, 3 pores are all immature. *15th leg*: about one-third of body-length, only slightly longer than 14th leg; tibia modified in male; accessory apical claw half the length of principal claw. *Male secondary sexual characters*: 14th tibia very swollen, more so internally and externally than dorsi-ventrally; distal half to two-thirds excavated dorsally with a feeble elevation half-way along the posterior (internal) edge of the excavation bearing a tuft of setae (Fig. 10); 15th tibia similarly though less markedly swollen; distal one-third excavated dorsally with a wart-like outgrowth projecting from the base of the excavation (Fig. 11). *Female gonopod*: coxa slightly excavated medially at base, with two conical spurs; claw simple; the external spur is much bigger than the internal which may be a feature of immaturity since all available females appear to be fourth post-larval stadia.



FIGS. 6–11. *Lithobius godmani*. Figs. 6 to 8. Ocelli. Fig. 9. Dental margin of prosternum, ventral. Fig. 10. Right 14th tibia of ♂, posterior (internal). Fig. 11. Right 15th tibia of ♂, posterior (internal).

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	mp	am	am	—	—	mp	ap	a
2	—	—	mp	amp	am	—	—	mp	ap	a
3–6	—	—	mp	amp	am	—	—	mp	ap	ap
7–10	—	—	mp	amp	am	—	—	amp	ap	ap
11	—	—	amp	amp	am	—	—	amp	ap	ap
12–14	—	m	amp	amp	am	a	—	amp	ap	ap
15	a	m	amp	amp	a	a	—	amp	ap	—

REMARKS. *Vulcanbius* was erected by Chamberlin (1944a) as a genus of Gosobiidae to receive species such as *L. godmani* showing conspicuous modification of the male 14th and 15th tibiae. But the genus was originally described as having the 14th tibia swollen, complanate and longitudinally furrowed, and the 15th tibia with a dorsal longitudinal ridge or crest. The latter part of this description hardly fits *L. godmani* and Chamberlin, who cannot have examined a specimen himself, may have misinterpreted Pocock's description.

Lithobius oedipes seems to be the name Pocock first gave to this species but he no doubt altered it to *godmani* before publication of his description, on realizing that the name was preoccupied by *L. oedipes* Bollman, 1888.

4. ***Lithobius salvini*** Pocock

(Figs. 12 to 16)

Lithobius salvini Pocock, 1895a : 7, Tab. 1 figs. 7, 7a–d.
Vulcanbius salvini : Chamberlin, 1944a : 201.

TYPE LOCALITY. Omilteme, Guerrero, Mexico.

MATERIAL EXAMINED. A jar labelled "*Lithobius salvini* Pocock, type, 1897.3.1.24–33" contains the following seven tubes :

"Omilteme 798". A fairly well-preserved male (Reg. no. 1897.3.1.25).

"Omilteme 798". Forty-one males, some immature and all more or less mutilated, of *L. salvini* together with a single mutilated male of *Neolithobius aztecus* (Humbert and Saussure). The specimen of *N. aztecus* (Reg. no. 1897.3.1.28) has now been separated from those of *L. salvini* (Reg. no. 1897.3.1.27).

"Omilteme 798". Five females, one of them immature (Reg. no. 1897.3.1.29).

"Omilteme 798". Two males and a female, all fairly well preserved, of *Lithobius humberti* Pocock (Reg. no. 1897.3.1.31–33).

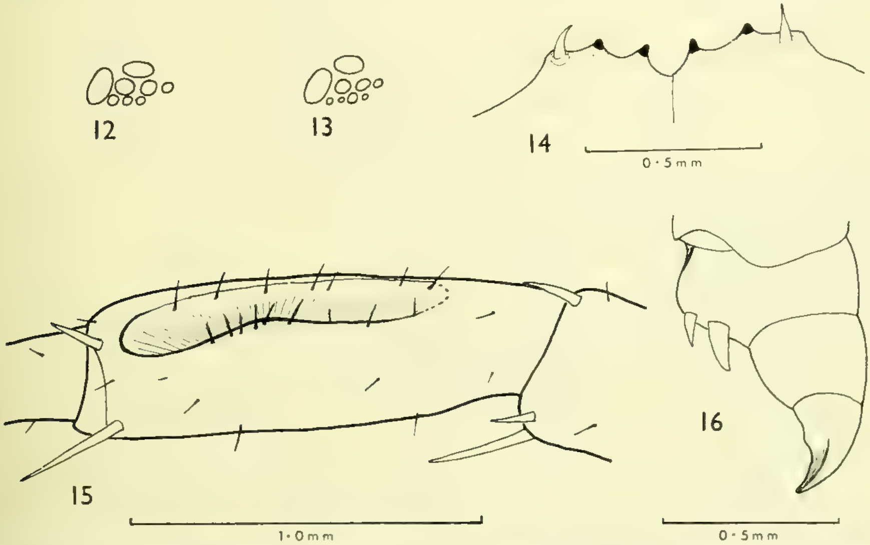
"Omilteme 811". Two bleached and desiccated females, one of them pierced longitudinally by a pin (Reg. no. 1897.3.1.30).

"Omilteme 818". A mutilated female (Reg. no. 1897.3.1.26).

"Omilteme 819". A fairly well-preserved male (Reg. no. 1897.3.1.24).

TYPE SPECIMEN. The best preserved specimen, a male 23 mm long, is here formally designated as the lectotype (Reg. no. 1897.3.1.24).

DESCRIPTION. *Size*: 18 to 25 mm long and 2·4 to 2·7 mm broad at T.8. *Colour*: brown. *Shape*: fusiform ; T.1 about as broad as T.3 ; body broadest at T.8. *Head*: broader than long, as broad as T.3. *Antennae*: half body-length or more, of 49 to 56 irregular articles. *Ocelli*: 1 + 1, 3, 3 or 1 + 1, 3, 4 (Figs. 12 and 13). *Prosternum*: with 2 + 2 (rarely 2 + 3) teeth ; lateral spine almost as stout as teeth at its base, setiform at apex in undamaged specimens, placed lateral to the lateral tooth at a distance rather less than the interval between lateral and medial teeth ; immediately adjacent to the insertion of the spine the anterior border forms a prominent rounded angle (Fig. 14) ; in some of the largest specimens the teeth are small so that the lateral spine appears relatively stouter. *Tergites*: posterior angles of T.8 angulated or blunt, those of T.10 angulated, those of T.12 and 14 angulated and slightly projecting ; posterior borders of T.1, 3 and 5 almost straight, those of T.8, 10 and 12 distinctly emarginate, that of T.14 straight or emarginate ; posterior angles of T.6 with well-developed rounded projections in some of the larger specimens only, but in most specimens including the lectotype they are simply rounded ; posterior angles of T.7 with broad blunt or angulated projections, those of T.9, 11 and 13 with broad sharp projections, the least broad on T.13 ; intermediate tergite straight or feebly emarginate posteriorly. *Coxal pores*: 4, 3, 3, 3 ; circular ; separated from one another by their own diameter or less ; one of the largest specimens has 5, 4, 4, 4 pores and the smaller specimens, all immature, have 3, 2, 2, 2. *15th leg*: a quarter to almost one-third of body-length, about the same length as 14th leg ; tibia slightly modified in male ; accessory apical claw half the length of principal claw. *Male secondary sexual characters*: 14th tibia moderately swollen, more so internally and externally than dorsi-ventrally, and excavated dorsally; the excavation may be limited to the distal one-third of the article or may be more extensive and is shallow proximally, becoming deeper distally, with an indefinite elevation along its posterior (internal) edge bearing an ill-defined group of setae (Fig. 15); 15th tibia slightly swollen with only a trace of dorsal excavation. *Female gonopod*: coxa slightly excavated medially at base, with two conical spurs; claw simple; the external spur is bigger than the internal and this seems to be an adult feature (Fig. 16).



FIGS. 12–16. *Lithobius salvini*. Figs. 12 and 13. Ocelli. Fig. 14. Dental margin of prosternum, ventral. Fig. 15. Left 14th tibia of ♂, posterior (internal). Fig. 16. Left ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	mp	am	a	—	—	mp	ap	a
2	—	—	mp	amp	am	—	—	mp	ap	a
3–5	—	—	mp	amp	am	—	—	mp	ap	ap
6	—	—	mp	amp	am	—	—	(a)mp	ap	ap
7–8	—	—	mp	amp	am	—	—	amp	ap	ap
9	—	(m)	(a)mp	amp	am	—	—	amp	ap	ap
10–11	—	(m)	amp	amp	am	—	—	amp	ap	ap
12–13	—	m	amp	amp	am	(a)	—	amp	ap	ap
14	—	m	amp	amp	am	a	—	amp	ap	ap
15	(a)	m	amp	amp	a	a	—	amp	(a)p	—

Letters in brackets indicate variable spines. Coxolateral spines (VaC) present in only a few specimens including the lectotype.

REMARKS. Chamberlin (1944a) included this species in *Vulcanbius* along with *L. godmani*; but as in the case of *godmani*, *salvini* agrees with Chamberlin's definition of the genus in respect of the 14th tibia but not of the 15th.

Pocock suspected that *godmani* and *salvini* might be no more than forms of the same species, but in spite of their similarity and almost identical spinulation they are sufficiently different to be regarded as distinct. Brölemann (1900) suggested that *Lithobius guatemalae* Brölemann might be identical with one or other of these species, but *guatemalae*, though probably closely related to both *godmani* and *salvini* cannot, from Brölemann's rather brief description, be regarded as identical with either.

5. ***Lithobius vulcani*** Pocock

(Figs. 17 to 21)

Lithobius vulcani Pocock, 1895a : 8, Tab. 1 figs. 8, 8a and b.
Labrobius vulcani : Chamberlin, 1915 : 536 ; 1921 : 9.
Vulcanbius vulcani : Chamberlin, 1944a : 201.
Sotimpius zilchi Kraus, 1954 : 300, Taf. 27 figs. 10–14.

TYPE LOCALITY. Volcan de Agua, Guatemala.

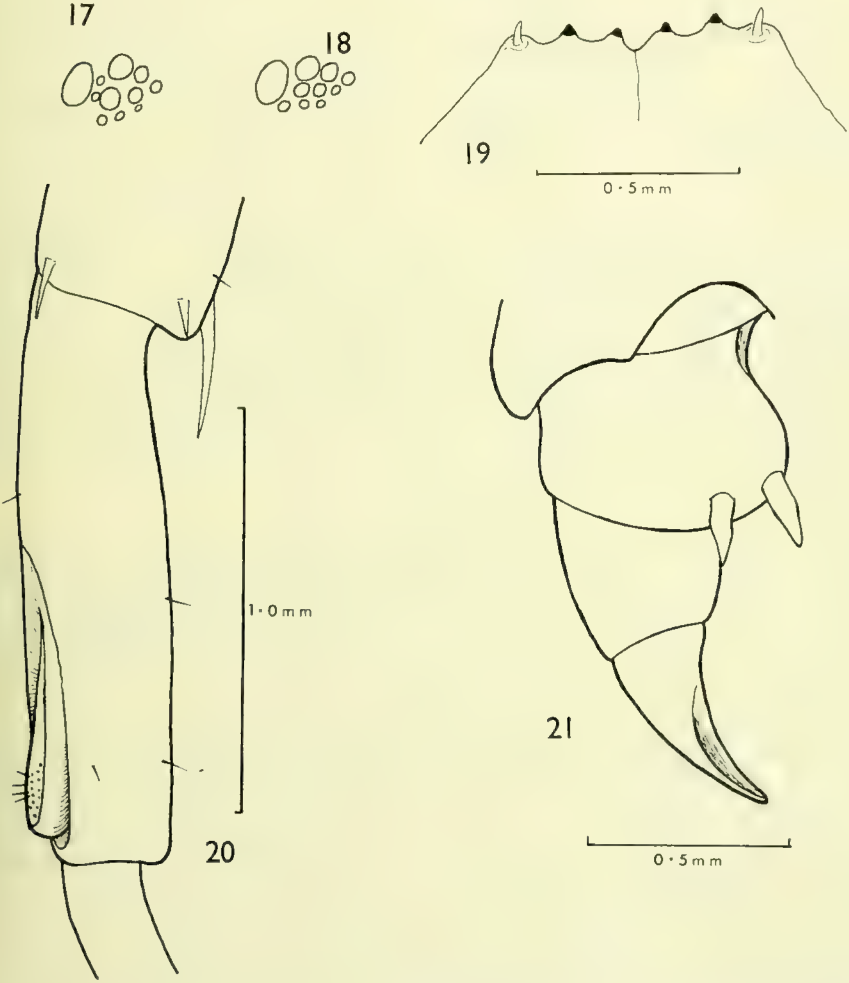
MATERIAL EXAMINED. A jar labelled " *Lithobius vulcani* Pocock type, 1894.4.1.72–73 " contains the following two tubes :

" Volcan de Agua ". A fairly well-preserved male (Reg. no. 1894.4.1.72).

Unlabelled. A female and an immature male, both fairly well preserved (Reg. no. 1894.4.1.73).

TYPE SPECIMEN. Pocock made it quite clear that his description was based on a single adult male, so that the above male labelled " Volcan de Agua " is the holotype (Reg. no. 1894.4.1.72).

DESCRIPTION OF HOLOTYPE. *Size*: 17·5 mm long and 2·2 mm broad at T.10. *Colour*: pale brown. *Shape*: fusiform ; T.1 rather narrower than T.3 ; body broadest at T.10. *Head*: broader than long, as broad as T.5. *Antennae*: 6·0 mm long, of 41 mostly transverse articles. *Ocelli*: 1 + 10 ; those of the main mass are irregular and cannot be represented by a formula (Fig. 17). *Prosternum*: with 2 + 2 teeth ; lateral spine less stout than teeth at its base, probably setiform at apex in undamaged specimens, placed about as far lateral to the lateral tooth as the interval between lateral and medial teeth ; immediately adjacent to the insertion of the spine the anterior border forms a distinct rounded angle (Fig. 19). *Tergites* : posterior angles of T.8 and 10 blunt, those of T.12 angulated, those of T.14 angulated and slightly projecting ; posterior borders of T.1, 3, 5 and 8 almost straight, those of T.10, 12 and 14 feebly emarginate ; posterior angles of T.9, 11 and 13 with triangular projections ; intermediate tergite straight posteriorly. *Coxal pores* : 4, 4, 4, 4 and 4, 4, 4, 3 ; circular ; separated from one another by more than their own diameter. *14th leg* : 4·6 mm long ; tibia slightly modified. *15th leg* : 5·2 mm long ; tibia modified ; accessory apical claw half the length of principal claw. *Male secondary sexual characters* : 13th tibia very slightly swollen ; 14th tibia moderately swollen, fusiform ; 15th tibia slightly swollen, excavated posterodorsally over rather more than its distal half ; from the base of the excavation rises a crest which becomes increasingly prominent distally and terminates abruptly just short of the distal end of the article (Fig. 20).



Figs. 17–21. *Lithobius vulcani*. Figs. 17 and 18. Ocelli. Fig. 19. Dental margin of prosternum, ventral. Fig. 20. Left 15th tibia of ♂, posterior (internal). Fig. 21. Right ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	p	m	am	—	—	p	a	a
2	—	—	p	m	am	—	—	p	ap	ap
3	—	—	p	am	am	—	—	mp	ap	ap
4	—	—	p	amp	am	—	—	mp	ap	ap
5	—	—	mp	amp	am	—	—	mp	ap	ap
6–9	—	—	mp	amp	am	—	—	amp	ap	ap
10–12	—	—	amp	amp	am	—	—	amp	ap	ap
13–14	—	m	amp	amp	am	—	—	amp	ap	ap
15	—	m	amp	amp	a	—	—	amp	p	—

Coxal spines (VaC and DaC) absent or broken. VmT of 5th leg (for example) over half the length of 5th tibia.

DESCRIPTION OF FEMALE. Differing from the male holotype in the following characters: *Size*: 19 mm long and 2·4 mm broad at T.10. *Antennae*: of 36 articles. *Ocelli*: 1 + 3, 3, 3 (Fig. 18). *Tergites*: posterior border of T.14 markedly emarginate; intermediate tergite relatively broad. *Coxal pores*: 6, 6, 6, 6 and 6, 6, 5, 5. *14th leg*: 5·8 mm long; tibia not modified. *15th leg*: 7·0 mm long; tibia not modified. *Spinulation*: coxolateral spine (VaC) present on 15; VmP absent on 5; VaF present on 1 and 2; DaC present on 15; DaP present on 5; DmP present on 1 and 2; DpF present on 1; DpT absent on 2. *Gonopod*: coxa markedly excavated medially at base, with two conical spurs separated from one another at their insertions by rather more than their own breadth; claw simple (Fig. 21).

DESCRIPTION OF IMMATURE MALE. Differing from the holotype in the following characters: *Size*: 14 mm long. *Antennae*: of 32 articles. *Ocelli*: as in female. *Tergites*: posterior angles of T.10 angulated, those of T.12 angulated and slightly projecting. *Coxal pores*: 3, 4, 4, 3. *Legs*: of much the same relative lengths as in holotype; no modification of 13th, 14th or 15th tibia. *Spinulation*: coxolateral spine (VaC) present on right 15th leg only; DaC present on both 15th legs; anterior limits of spine-series not recorded.

REMARKS. *Labrobius* was erected by Chamberlain (1915) as a genus of Gosobiidae to receive a number of species, including *L. vulcani*, showing a conspicuous crest on the male 15th tibia; but he later restricted the genus to exclude those species showing obvious modification of any other article (Chamberlin 1943). *L. vulcani* seems to be the only one of Pocock's Central American species of *Lithobius* which Chamberlin actually examined himself and he must finally have decided that the swelling of the male 14th tibia was sufficient grounds for excluding it from *Labrobius* and including it in *Vulcanbius* (Chamberlin 1944a). But there is only moderate swelling of the 14th tibia in the holotype without any sulcus or excavation, and Kraus (1954) found only slight dorsal flattening of this article in *zilchi* (=*vulcani*). *L. vulcani*, therefore, agrees with *Vulcanbius* in the structure of the 15th tibia but not in that of the 14th and there seems little reason for including it in the same species-group as *L. godmani* and *L. salvini*, where the opposite obtains (see p. 47), on the basis of the structure of the 14th and 15th legs.

Kraus (1954) saw no reason for separating *zilchi* generically from a number of species of *Sotimpius* (*sensu* Chamberlin) he described from El Salvador. He distinguished it from *vulcani* by means of its more numerous ocelli, the very long ventral spines on the tibiae of the foremost legs, and the more numerous setae on the male 15th tibial crest. In fact, Pocock understated the number of ocelli in the holotype of *vulcani* and made no special mention of the length of the ventral tibial spines (VmT) which are just as long on the foremost legs of the holotype as those described by Kraus for *zilchi*. The setae on the 15th tibia of the holotype (Fig. 20) are certainly meagre compared with those illustrated by Kraus in a comparable figure of *zilchi* (Kraus 1954 : Taf. 27 fig. 13); but many of them have obviously been lost and had probably been lost before Pocock drew his figure (Pocock 1895a : Tab. 1 fig. 8b) which was all Kraus had to guide him. There is little doubt that *zilchi* and *vulcani* are identical.

It is possible that the female and immature male in the unlabelled tube belong to a species other than *L. vulcani* because of the different arrangement of the ocelli and the presence of the coxal spines VaC and DaC on the 15th legs. However, Kraus mentioned the variability of the ocelli in *zilchi* and figured an arrangement (Kraus 1954 : Taf. 27 fig. 11) very similar to that found in these two specimens (Fig. 18): he found no coxal spines and the probabilty is that these spines are variable in *L. vulcani* and that all three of Pocock's specimens are conspecific.

6. ***Lithobius pontifex*** Pocock

(Figs. 22 to 24)

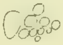
Lithobius pontifex Pocock, 1895a : 5, Tab. 1 figs. 4, 4a–d.
Arenobius (*Kunobius*) *pontifex* : Chamberlin, 1912 : 178.
Guerrobius pontifex : Chamberlin, 1942 : 20.

TYPE LOCALITY. Amula, Guerrero, Mexico.

MATERIAL EXAMINED. A jar labelled "*Lithobius pontifex* Pocock, type, 1897.3.1.15 Amula, 6,000′, Godman and Salvin, Biol. Centr. Amer." contains a tube labelled "Amula 1085". A male with most of the legs missing and the right 15th leg separate in a microvial.

TYPE SPECIMEN. Pocock's description is of a single male and the above specimen is the holotype (Reg. no. 1897.3.1.15).

DESCRIPTION OF HOLOTYPE. *Size*: 27 mm long and 3·8 mm broad at T.5. *Colour*: dark brown. *Shape*: attenuated posteriorly; T.1 narrower than T.3; body broadest at T.5. *Head*: broader than long, narrower than T.1, about as broad as T.12. *Antennae*: 12 mm long, of 52 and 55 irregular articles. *Ocelli*: 1 + 1, 3, 4, 1 (Fig. 22). *Prosternum*: with 2 + 2 small teeth; lateral spine pigmented, short and blunt, much stouter than teeth, placed further lateral to the lateral tooth than the interval between lateral and medial teeth; lateral to the spine the anterior border forms a feeble rounded angle; median cleft very shallow (Fig. 23). *Tergites*: posterior angles of T.8 blunt, those of T.10 angulated, those of T.12 and 14 angulated and slightly projecting; posterior borders of large tergites only feebly emarginate; posterior angles of T.6 with distinct rounded projections, those of T.7 with rather broader rounded projections, those of T.9, 11 and 13 with broad sharp projections; intermediate tergite very feebly emarginate posteriorly. *Coxal pores*: 5, 4, 4, 4; circular or somewhat reniform; separated from one another by less than their own diameter. *15th leg*: 7·4 mm long, about the same length as 13th leg; according to Pocock much shorter than 14th leg which is now missing; tibia and tarsus modified; accessory apical claw half the length of principal claw. *Male secondary sexual characters*: 14th leg unmodified according to Pocock; 15th femur with a feeble dorsal sulcus; 15th tibia very swollen, excavated posterodorsally with a flat wart-like outgrowth occupying most of the excavation; 15th tarsus even more swollen, extensively and deeply excavated posterodorsally (Fig. 24).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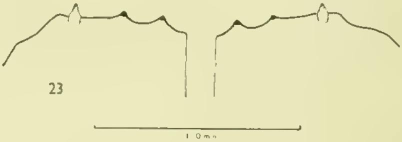
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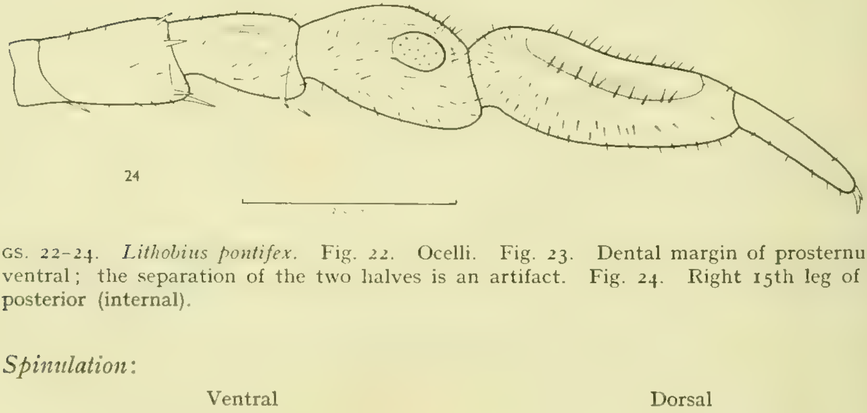
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FIGS. 22–24. *Lithobius pontifex*. Fig. 22. Ocelli. Fig. 23. Dental margin of prosternum, ventral; the separation of the two halves is an artifact. Fig. 24. Right 15th leg of ♂, posterior (internal).

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
13	—	m	amp	amp	am	a	—	amp	ap	ap
15	—	m	amp	amp	a	a	—	amp	—	—

REMARKS. Chamberlin (1912) erected *Arenobius* to receive most of the species then known to him which he later (1915) assigned to the Gosobiidae. *Kunobius* (Chamberlin 1912) was erected as a subgenus of *Arenobius* to receive such species as *L. pontifex* and *L. humberti* Pocock which, while having some modification of the male 15th legs, have the 14th legs unmodified. Chamberlin made no mention of

Kunobius in any of his writings subsequent to 1912 and redefined *Arenobius* (Chamberlin 1917) to exclude all species other than the type species *L. manegitus* Chamberlin. He later erected *Guerrobius* (Chamberlin 1942), characterized quite positively by conspicuous modification of the male 15th tibia and tarsus, to receive *L. pontifex* and *L. humberti* with *pontifex* as type species. But in a more recent definition of *Guerrobius* (Chamberlin 1943) he restricted it to those species with relatively slender lateral prosternal spines, thus excluding the type species. This lapse on Chamberlin's part must have been due to his misinterpretation of Pocock's description of *L. pontifex*.

7. ***Lithobius humberti*** Pocock

(Figs. 25 to 29)

Lithobius humberti Pocock, 1895a : 5, Tab. 1 figs. 5, 5a–c.
Arenobius (*Kunobius*) *humberti* : Chamberlin, 1912 : 178.
Guerrobius humberti : Chamberlin, 1942 : 20.

TYPE LOCALITY. Omilteme, Guerrero, Mexico.

MATERIAL EXAMINED. A jar labelled "*Lithobius humberti* Pocock, type, 1897.3.1.21–23" contains the following two tubes:

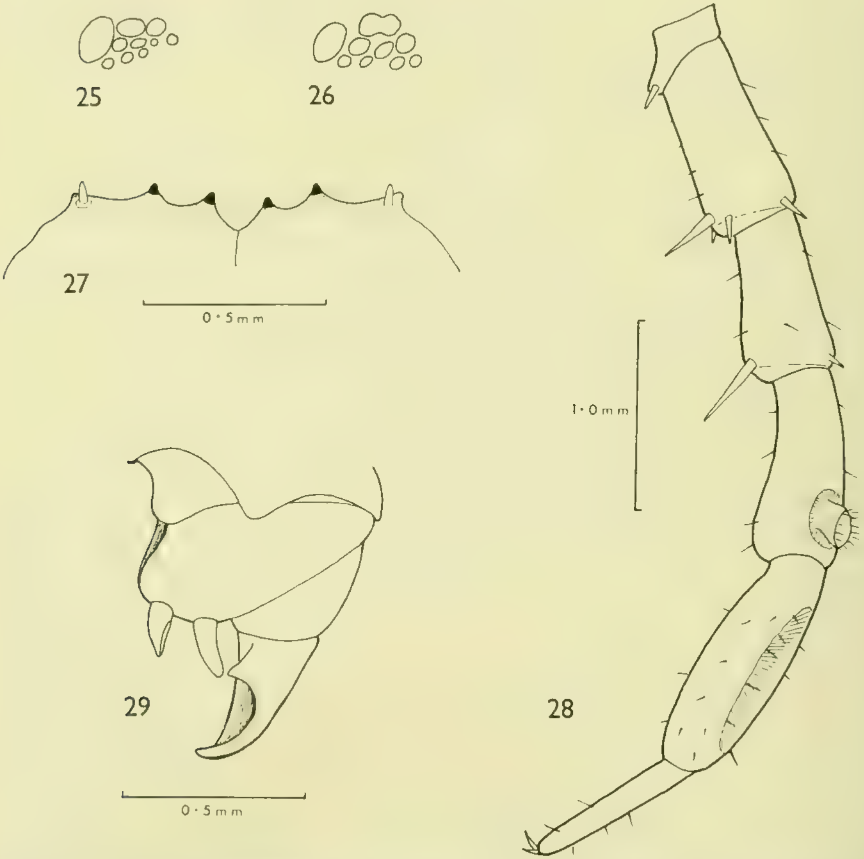
"Omilteme 703". A rather mutilated male (Reg. no. 1897.3.1.21).

"Omilteme 703". A mutilated female of *L. humberti* together with an immature male of *L. salvini*. The specimen of *L. humberti* (Reg. no. 1897.3.1.22) has now been separated from that of *L. salvini* (Reg. no. 1897.3.1.23).

The three specimens of *L. humberti* (Reg. no. 1897.3.1.31–33) originally placed in the jar with those of *L. salvini* (see p. 48) have also been examined.

TYPE SPECIMEN. Pocock's description was based on two males and a female and the presumption is that the specimens in the jar labelled "*Lithobius humberti*" are the syntypes, in spite of the fact that one was misdetermined and the others are in poor condition. The adult male, 18 mm long with the left 15th leg missing, is here formally designated as the lectotype (Reg. no. 1897.3.1.21). Much of the following description, however, is based on the misplaced specimens which are in better condition.

DESCRIPTION. *Size*: 15 to 18 mm long and 2·2 to 2·6 mm broad at T.8. *Colour*: dark brown. *Shape*: feebly fusiform; T.1 rather narrower than T.3; body broadest at T.5 or 8. *Head*: as broad as long, about as broad as T.3. *Antennae*: usually over half body-length, of 50 to 52 irregular articles, but in the lectotype barely one-third of body-length with 38 articles. *Ocelli*: 1 + 2, 4, 3 or 1 + 1, 3, 4 (Figs. 25 and 26). *Prosternum*: with 2 + 2 teeth; lateral spine less stout than teeth at its base, peg-like, placed further lateral to the lateral teeth than the interval between lateral and medial teeth; immediately adjacent to the insertion of the spine the anterior border forms a fairly sharp angle (Fig. 27). *Tergites*: as in *L. pontifex* but the posterior projections on T.7 are broader and less evenly rounded. *Coxal pores*: 4, 4, 3, 3; 4, 4, 4, 3 or 5, 4, 4, 3 in males; 5, 4, 4, 4 in females; circular; separated from one another by their own diameter. *15th leg*: barely exceeding a quarter of body-length, rather shorter than 14th leg in males; about two-fifths of body-length, longer than 14th leg in females; tibia and tarsus modified in male; accessory apical claw half the length of principal claw. *Male secondary sexual characters*: 14th leg unmodified; 15th tibia slightly swollen distally, with a circular excavation on the posterodorsal aspect of its distal one-third, from which projects a prominent wart-like outgrowth; 15th tarsus more markedly swollen, extensively excavated posterodorsally (Fig. 28). *Female gonopod*: coxa slightly excavated medially at base, with two fairly stout spurs separated from one another at their insertions by their own breadth; claw simple with a conspicuous tooth at its base (Fig. 29).



Figs. 25–29. *Lithobius humberti*. Figs. 25 and 26. Ocelli. Fig. 27. Dental margin of prosternum, ventral. Fig. 28. Right 15th leg of ♂, posterior (internal). Fig. 29. Left ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	m	m	—	—	mp	a	—
2	—	—	p	amp	am	—	—	mp	ap	a
3–7	—	—	mp	amp	am	—	—	mp	ap	ap
8–11	—	—	amp	amp	am	—	—	amp	ap	ap
12–14	—	m	amp	amp	am	—	—	amp	ap	ap
15	—	m	amp	am	a	a	—	amp	ap	—

The above is the usual spinulation but, on the 15th legs, DaC may be absent and in the only female with these legs intact VpF, DaT and DpT are present.

REMARKS. The history of the generic classification of *L. humberti* is the same as that of *L. pontifex*. These two species are very close to one another and there is every reason for including them in the same species-group, in spite of the fact that the female of *L. pontifex* is unknown.

8. ***Lithobius stolli*** Pocock

(Figs. 30 to 32)

Lithobius stolli Pocock, 1895a : 9, Tab. 1 figs. 10, 10a–c.
Arenobius (*Sowubius*) *stolli* : Chamberlin, 1912 : 178.
Sowubius stolli : Chamberlin, 1921 : 10.

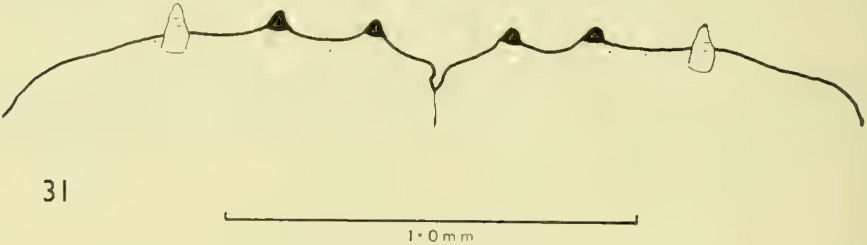
TYPE LOCALITY. Volcan de Agua, Guatemala.

MATERIAL EXAMINED. A jar labelled " *Lithobius stolli* Pocock, type, 1894.4.1.76 " contains a tube labelled " Volcan de Agua 9,000–10,000′ ". A female of *Lithobius castaneus* Newport, 1844, fairly well preserved but with the 15th legs missing.

TYPE SPECIMEN. Pocock's description is of a single female and the above specimen is the holotype (Reg. no. 1894.4.1.76).

DESCRIPTION OF HOLOTYPE. *L. castaneus* is a well-known Mediterranean species but this specimen differs in detail from Brölemann's (1930) account and is therefore described below.

Size: 27 mm long and 3·8 mm broad at T.10. *Colour*: brown with a darker dorsal median band on the more posterior tergites. *Shape*: almost parallel-sided; T.1 broader than T.3; body broadest at T.10. *Head*: rather longer than broad, as broad as T.1; a pair of short faint paramedian sulci run forwards on either side from the posterior marginal sulcus. *Antennae*: 12·2 mm long, of 27 elongate articles, each article being two or three times longer than broad. *Ocelli*: 1 + 5, 5, 6, 6, 4 (Fig. 30). *Prosternum*: with 2 + 2 small teeth; lateral spine short and blunt, stouter than teeth, placed as far lateral to the lateral tooth as the interval between lateral and medial teeth; lateral to the spine the anterior border forms a broad level shoulder before sloping backwards without angulation; median cleft essentially shallow with a minute secondary cleft in the mid-line (Fig. 31). *Tergites*: large tergites with posterior angles rounded and posterior borders emarginate; posterior angles of T.9 and 11 squared, those of T.13 with traces of projections; on T.1, 3 and 5 the marginal sulcus is interrupted posteriorly and curved forwards on either side; this sculpturing is repeated faintly on T.8, 10 and 12; intermediate tergite quite strongly emarginate posteriorly. *Coxal pores*: 9, 9, 9, 9; oval to oblong. *14th leg*: 9·2 mm long; accessory apical claw a quarter the length of principal claw. *15th leg*: missing; according to Pocock the accessory apical claw is absent. *Gonopod*: coxa without trace of medial excavation at base, with two short acuminate spurs separated from one another at their insertions by barely their own breadth; claw simple (Fig. 32).



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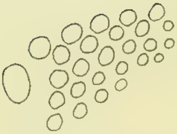

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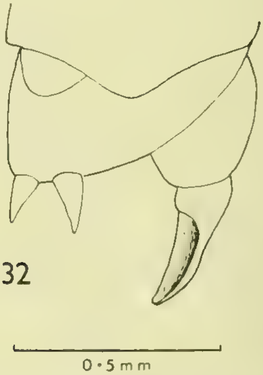

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FIGS. 30–32. *Lithobius stolli*. Fig. 30. Ocelli. Fig. 31. Dental margin of prosternum, ventral. Fig. 32. Left ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	mp	amp	am	—	—	amp	ap	ap
2–11	—	—	amp	amp	am	—	—	amp	ap	ap
12	—	m	amp	amp	am	a	—	amp	ap	ap
13	a	m	amp	amp	am	a	—	amp	ap	ap
14	a	m	amp	amp	am	a	—	amp	ap	p
15	a	1	3	2	1	a				

On the 14th leg VaT and DaF are present on one side only. The numerals indicate the ventral spinulation given by Pocock for the telopodite of the 15th leg.

REMARKS. *Sowubius* was erected by Chamberlin (1912) as a monotypic subgenus of *Arenobius*, characterized by the absence of posterior tergal projections and the absence of a 15th accessory apical claw, to receive *L. stolli*. It was later raised to a genus (Chamberlin 1921). Pocock's illustration of the gonopod of *L. stolli* shows no trace of basal constriction of the coxa (Pocock 1895a : Tab. 1 fig. 10c) and Chamberlin had, therefore, little justification for including this species in *Arenobius* and later in the Gosobiidae (see p. 44). Pocock's illustration is, however, on too small a scale to show the detailed structure of the gonopod and Chamberlin may have assumed the base of the coxa to be excavated as it is in the majority of neotropical forms : he may also have been influenced by the simple genital claw, another feature he regarded as characteristic of the Gosobiidae, which is clearly shown in Pocock's illustration.

The holotype of *L. stolli* has been compared with a number of examples of *L. castaneus* from Europe and North Africa and also with the holotype of *L. castaneus* Newport in the British Museum (Natural History) (see also Eason 1972) and there is no doubt as to its identity. *Sowubius* thus becomes the senior synonym of *Euporodontus*, a genus erected by Verhoeff (1942) with *L. castaneus* Newport as type species.

In view of the historical association between Central America and Spain, where *L. castaneus* is common, artificial introduction seems the most likely explanation of the presence of this species in Guatemala.

9. ***Lithobius provocator*** Pocock

Lithobius provocator Pocock, 1891a : 152 ; 1893 : 122 ; Chamberlin, 1904 : 653 ; 1920a : 280, Pl. xxix figs. 6–8.
Eremobius provocator : Chamberlin, 1925 : 408.

TYPE LOCALITY. Bermuda.

MATERIAL EXAMINED. A jar labelled "*Lithobius provocator* Pocock, type, Bermuda, Challenger" contains two females, two adult males and an immature male, all more or less mutilated, belonging to *Lithobius peregrinus* Latzel, 1880 (Reg. no. 1892.12.1.16–20).

TYPE SPECIMENS. All the above specimens are syntypes.

DESCRIPTION. The specimens are all quite typical and answer to Chamberlin's (1920a) description of *L. provocator* and Brölemann's (1930) description of *L. peregrinus*. The position of the lateral prosternal spines medial to the respective lateral teeth in *peregrinus* was not made clear by Brölemann but was adequately described and figured by Matic (1957 : 13, figs. 4 and 5).

REMARKS. Pocock (1893) realized that this was not an "Antillean" species and suspected that it might be a form of the European *L. forficatus* (Linn.). Chamberlin (1920a) gave a full description of *L. provocator* based on Bermudan material and later (Chamberlin 1925) erected *Eremobius* as a monotypic genus, characterized by the arrangement of the prosternal spine and teeth, to receive it. Synonymy of *L. provocator* with *L. peregrinus* was first proposed by Jeekel (1963).

Lithobius ethochaetus, which was described from a single female taken at New Orleans in a cargo from Panama (Chamberlin 1938), undoubtedly belongs to *L. peregrinus.* A record of *peregrinus* from an inland locality in South Africa (Attems 1928) is further evidence of the extent to which this species, whose natural range is in southern and central Europe, has been artificially spread.

10. ***Lithobius sydneyensis*** Pocock

(Figs. 33 to 36)

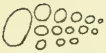
Lithobius sydneyensis Pocock, 1891a : 153 ; Attems, 1914 : 97.
Lithobius bermudensis Pocock, 1893 : 126.
Walesobius sydneyensis : Chamberlin, 1920b : 77 ; Archey, 1937 : 72, Pl. 16 figs. 1–6.
Lithobius araïchensis Brölemann, 1924a : 58, figs. 4–6 ; 1924b : 187 ; 1932 : 55 ; Matic, 1959 : 18, fig. 3 ; 1968 : 71 ; Demange, 1962 : 138 ; Matic *et al.*, 1967 : 192.
Walesobius excrescens Attems, 1928 : 78.
? *Lithobius platensis* Gervais : Silvestri, 1899 : 142.
? *Chilebius coquimbo* Chamberlin, 1955 : 56.
? *Andebius callao* Chamberlin, 1955 : 57.

TYPE LOCALITY. Sydney, Australia.

MATERIAL EXAMINED. A jar labelled "*Lithobius sydneyensis* Pocock, type, Sydney, Brazier" contains a male and a female, both well preserved, and two mutilated males, one of them immature (Reg. no. 1972.738–740).

TYPE SPECIMEN. The well-preserved male, 15 mm long, is here formally designated as the lectotype and has now been placed in a separate tube (Reg. no. 1972.738).

DESCRIPTION. *Size*: 15 to 19 mm long and 2·0 to 2·4 mm broad at T.10. *Colour*: pale brown. *Shape*: fusiform ; T.1 as broad as T.3 or rather broader ; body broadest at T.8 or 10. *Head*: barely broader than long, as broad as T.5. *Antennae*: two-fifths of body-length, of 26 to 28 slightly elongate fairly regular articles. *Ocelli*: 1 + 5, 5, 3 (Fig. 33) or, on the left side of the female, 1 + 6, 5, 4, 2. *Prosternum*: with 2 + 2 teeth, the medial tooth the larger ; lateral spine setiform but stouter than the largest seta, placed posterolateral to lateral tooth ; lateral to the spine the anterior border forms an irregular shoulder (Fig. 34). *Tergites*: posterior angles of T.8 and 10 rounded or blunt, those of T.12 blunt, those of T.14 rounded or blunt ; posterior borders of large tergites moderately emarginate ; posterior angles of T.9, 11 and 13 with triangular projections ; intermediate tergite emarginate posteriorly. *Coxal pores*: 6, 7, 6, 5 or 6, 7, 7, 5 (5, 5, 6, 5 in immature male) ; oval or slightly oblong. *15th leg*: about two-fifths of body-length ; femur modified in male ; accessory apical claw very small, a fifth to a quarter the length of principal claw. *Male secondary sexual characters*: the dorsal aspect of the distal end of the 15th femur bears a prominent wart-like outgrowth arising from a shallow circumscribed depression (Fig. 35). *Female gonopod*: coxa with two long slender spurs separated from one another at their insertions by about their own breadth ; the spurs appear acuminate when viewed laterally but blunt and somewhat serrated apically when viewed ventrally ; claw with a large internal (dorsal) denticle and a much smaller external (ventral) denticle (Fig. 36).



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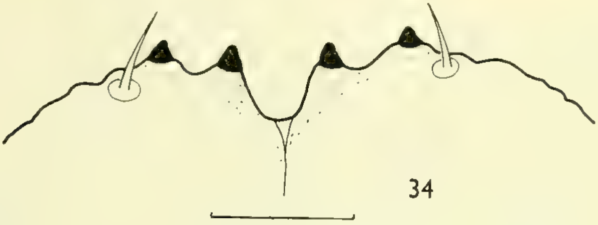

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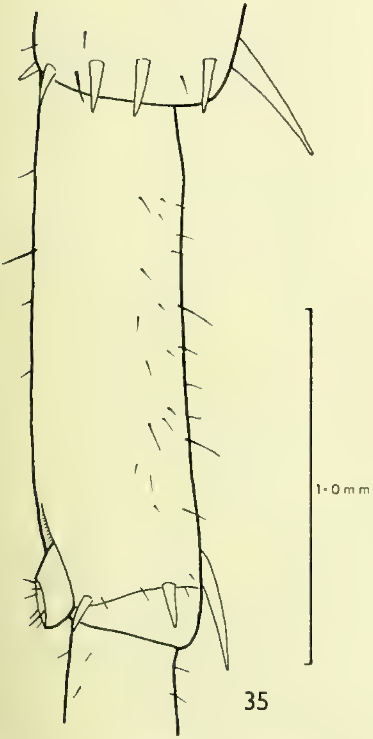

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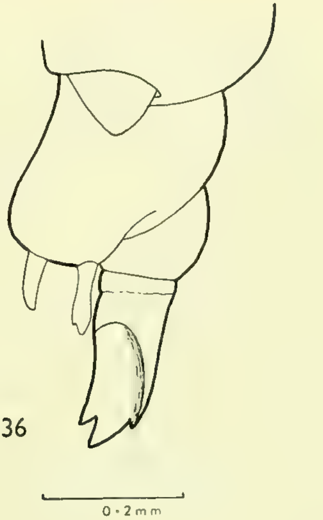

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FIGS. 33–36. *Lithobius sydneyensis.* Fig. 33. Ocelli. Fig. 34. Dental margin of prosternum, ventral. Fig. 35. Left 15th femur of ♂, posterior (internal). Fig. 36. Left ♀ gonopod, ventral.

Spinulation of lectotype (male) :

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1–2	—	—	mp	amp	am	—	—	mp	ap	a
3–9	—	—	mp	amp	am	—	—	mp	ap	ap
10–11	—	—	mp	amp	am	—	—	amp	ap	ap
12	—	—	amp	amp	am	—	—	amp	ap	ap
13	—	m	amp	amp	am	a	—	amp	p	ap
14	—	m	amp	amp	a	a	—	amp	p	p
15	—	m	amp	amp	a	a	—	amp	p	p

In addition to the above there are two supplementary posterior prefemoral spines on each 15th leg (Fig. 35); VaF is duplicated on the right 15th leg.

In the female 1VmP, 15VpF, 14DpT, 15DpF and 15DpT are absent; 12VmT, 2DpT and 9DaP are present; the two supplementary prefemoral spines are present on the 15th legs but 15VaF is simple on both sides.

REMARKS. *Walesobius* was erected by Chamberlin (1920b) as a monotypic genus, characterized by the male 15th femoral protuberance, to receive *L. sydneyensis*.

Although Brölemann's (1924a) description of *L. araichensis* from Morocco differs from Pocock's specimens of *L. sydneyensis* in the smaller number of ocelli (9 to 11), the circular coxal pores, and the presence of only one supplementary prefemoral spine on the 15th leg, examples of both sexes of *araichensis* from Gibraltar in the Collection of the Cave Research Group of Great Britain in the British Museum (Natural History) have been compared with those of *sydneyensis* and there is no doubt that the two forms are conspecific. *Walesobius excrescens* from Cape Town (South Africa) was described by Attems (1928) as having coxal pores exactly as in the Gibraltan specimens (4, 5, 5, 3; circular), a simple 15th apical claw and the large ocellus anterior to the smaller ocelli (10 + 1): but the 15th accessory apical claw is very small in *sydneyensis* and was overlooked by both Pocock and Archey (1937), and Attems' description of the ocelli may well have suffered mistranslation as the arrangement he gave is so unusual as to be barely credible: there is little doubt that *sydneyensis* and *excrescens* are conspecific. *Lithobius platensis* Gervais as described by Silvestri (1899), *Chilebius coquimbo* (Chamberlin 1955) and *Andebius callao* (Chamberlin 1955) cannot be separated from *L. sydneyensis* by their rather brief descriptions, but their identity is less certain. Synonymy of *L. bermudensis* Pocock from Bermuda with *L. sydneyensis* is discussed below (p. 63).

This species, as well as occurring in Morocco and Gibraltar, is widespread in southern Spain (Matic 1959, 1968). If we assume that this is its natural range and that it has been introduced to Bermuda, it might also have been spread artificially along the trade-routes to such seaports as Sydney, Auckland (New Zealand), where it was discovered by Archey (1937), and Cape Town. This suggestion is supported by the fact that there are few, if any, indigenous species of Lithobiidae in Australasia or South Africa in both of which regions the Lithobiomorpha is represented almost exclusively by the Henicopidae.

Lithobius platensis (*sensu* Silvestri) was recorded by Silvestri (1905) from Quinta Normal (Chile), Buenos Aires (Argentina) and Montevideo (Uruguay), while *Chilebius coquimbo* and *Andebius callao* were recorded from Coquimbo (Chile) and Callao (Peru) respectively by Chamberlin (1955). It is possible that these records, all from seaports or coastal localities, also refer to *L. sydneyensis*; but an indigenous species of Lithobiidae is known to occur in South America (Turk 1955) and *L. platensis* (which is probably conspecific with *Chilebius coquimbo* and *Andebius callao*) may be another.

11. ***Lithobius bermudensis*** Pocock

Lithobius bermudensis Pocock, 1893: 126.

TYPE LOCALITY. Bermuda.

MATERIAL EXAMINED. A jar labelled "*Lithobius* (s.s.) *bermudensis* Pocock, Bermuda, Challenger, 92.12.1.21" contains a female of *Lithobius sydneyensis* Pocock which is shrivelled, deeply pigmented and broken in two.

TYPE SPECIMEN. Pocock's description is of a single female and the above specimen is the holotype (Reg. no. 1892.12.1.21).

DESCRIPTION OF HOLOTYPE. The specimen is very defective and the following description is necessarily rather incomplete, but it is so close to Brölemann's (1924a) description of *L. araichensis* (=*sydneyensis*) and the Gibraltan examples of this species which have been examined (see p. 62) that there is little doubt as to its identity.

Length: about 14 mm. *Antennae*: broken. *Ocelli*: 1 + 4, 3, 2. *Prosternum*: with 2 + 2 teeth and distinct shoulders lateral to the lateral spines. *Tergites*: somewhat distorted but the general shape of the tergites and the posterior projections on T.9, 11 and 13 are as in *L. sydneyensis*. *Coxal pores*: 4, 5, 5, 4; circular. *15th leg*: the apical claw has been broken off, but Pocock noted the presence of an accessory claw. *Female gonopod*: as in *L. sydneyensis*.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	amp	a	a	—	amp	p	p
15	—	m	amp	am	a	a	—	amp	p	—

In addition to the above there is a single supplementary posterior prefemoral spine on each 15th leg.

REMARKS. Pocock realized that *L. bermudensis*, like *L. provocator*, was not an "Antillean" species but he was unable to identify it with any species known to him. Chamberlin (1920a) believed it to be an immature stadium of *L. provocator* (=*peregrinus*). The fact that it proves to be *L. sydneyensis* is not surprising as we have already seen how this species seems to have spread far beyond its natural range in the western Mediterranean (see p. 62). Bollman's (1889) doubtful record of *L. lapidicola* Meinert from Bermuda may also refer to *L. sydneyensis*.

12. ***Lithobius persicus*** Pocock

(Figs. 37 and 38)

Lithobius persicus Pocock, 1899 : 399.
Alokobius persicus : Attems, 1927 : 245.

TYPE LOCALITY. Seir, Persia.

MATERIAL EXAMINED. A jar labelled "*Lithobius persicus* Pocock, type, 1900.1.15.2" contains a tube labelled "Seir 18.viii, coll. by R. T. Gunther". A male pierced longitudinally by a pin.

TYPE SPECIMEN. Pocock's description is of a single male and the above specimen is the holotype (Reg. no. 1900.1.15.2).

DESCRIPTION OF HOLOTYPE. *Size*: 19 mm long and 2·2 mm broad at T.10. *Colour*: dull brown. *Shape*: almost parallel-sided; T.1 rather narrower than T.3; body broadest at T.10. *Head*: distorted but probably broader than T.1; frontal sulcus very marked. *Antennae*: 7·0 mm long, of 47 articles. *Ocelli*: 1 + 5, 4, 3, 2 (Fig. 37). *Prosternum*: with 2 + 2 teeth; lateral spine slender but stouter than setae, placed immediately posterolateral to lateral tooth; lateral to the spine the anterior border appears to slope backwards without formation of shoulders, but its detailed structure is obscured owing to its being damaged by the pin. *Tergites*: posterior angles of T.8 and 10 rounded, those of T.12 and 14 blunt; posterior borders of large tergites feebly emarginate; posterior angles of T.9 obtuse, those of T.11 with feeble projections, those of T.13 with more marked projections (Fig. 38); intermediate tergite moderately emarginate posteriorly. *Coxal pores*: 3, 4, 4, 4; circular; separated from one another by more than their own diameter. *14th leg*: with an accessory apical claw. *15th leg*: 5·5 mm long; accessory apical claw absent. *Male secondary sexual characters*: 14th tibia not sulcate although Pocock mentioned a dorsal sulcus on this article; 14th femur with a feeble dorsal sulcus; 15th tibia with a distinct shallow dorsal sulcus.

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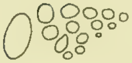

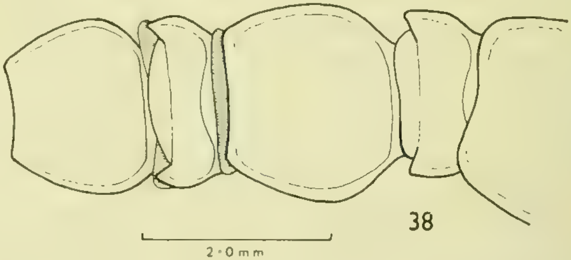

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FIGS. 37–38. *Lithobius persicus*. Fig. 37. Ocelli. Fig. 38. 11th to 14th tergites, dorsal.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	mp	amp	amp	—	—	mp	ap	—
2–11	—	—	mp	amp	amp	—	—	amp	ap	ap
12	—	—	amp	amp	amp	—	—	amp	ap	ap
13	—	m	amp	amp	am	a	—	amp	ap	ap
14	a	m	amp	amp	am	a	—	amp	p	p
15	a	m	amp	amp	am	a	—	amp	p	—

REMARKS. *Alokobius* was erected by Attems (1926) to receive species such as *L. persicus* with some modification of the male 14th or 15th tibiae; it was later reduced to a subgenus of *Lithobius* (Attems 1938) and most authors disregard it altogether.

L. persicus is not easily recognizable from Pocock's description which gives 42 antennal articles, a dorsal sulcus on the 14th as well as the 15th tibia, and square posterior angles on T.11; but no species resembling the holotype at all closely has been rediscovered in spite of fairly extensive collecting in Persia and Iraq (Brölemann 1922, 1923; Attems 1951; Chamberlin 1958; Matic 1969). The species probably belongs to the same group as *L. laccatus* Attems, 1951 and *L. easoni* Matic, 1969.

13. ***Lithobius doriae*** Pocock

Lithobius (*Archilithobius*) *doriae* Pocock, 1890 : 63.
Lithobius doriae : Brölemann, 1898 : 190; Verhoeff, 1937a : 203; Matic, 1970 : 37.
Lithobius mediterraneus Chalande, 1903 : 221; 1905 : 72.
Lithobius pilicornis doriae : Brölemann, 1930 : 299, and most subsequent authors.
Lithobius doriae uccianensis Verhoeff, 1943 : 15.

TYPE LOCALITIES. Busalla, Finale and Isoverde, Italy.

MATERIAL EXAMINED. A jar labelled "*Archilithobius doriae* (Pocock), type, 1889.3.8.25–26" contains the following two tubes:

"*Lith.* (*Arch.*) *busallae* (Pocock), Finale, O. Thomas (c & p)." An immature female (Reg. no. 1889.3.8.25).

"*Lith.* (*Arch.*) *busallae* (Pocock), Busalla, O. Thomas (c & p)" [the word 'busallae' has been crossed out and 'doriae' substituted]. Five males and seven females of *L. doriae* together with a female of *Lithobius castaneus* Newport and a female of *Lithobius piceus verhoeffi* Demange (Reg. no. 1889.3.8.26). The last two specimens have now been separated from those of *L. doriae*.

TYPE SPECIMEN. Pocock's description was based on a number of specimens from Busalla, one from Finale and one from Isoverde (all in Liguria, Italy), the last of which has not been found. The best preserved specimen from Busalla, a male 17 mm long, is here formally designated as the lectotype and has now been placed in a separate tube (Reg. no. 1889.3.8.26 (part)).

DESCRIPTION. In general agreement with Brölemann's (1930) description of *L. pilicornis doriae*. Of the variable features, the prosternal teeth are usually 4 + 4 but four specimens have 4 + 5, 4 + 6, 5 + 5 and 5 + 7 teeth respectively; the posterior angles of T.13 have small but distinct projections, and in a few specimens those of T.11 have very feeble projections; the coxal pores are usually 5, 6, 6, 5 or 5, 7, 7, 5, oblong in the larger and oval or almost circular in the smaller specimens; on the 15th leg the spines VaC (coxolateral) and VmC are always present; on the 14th leg VaC is present in most specimens and VmC in one only.

REMARKS. The subgenus *Archilithobius* in which Pocock placed *L. doriae* was erected by Stuxberg (1875) to receive all those species without marked posterior tergal projections: it is now disregarded by most authors but Attems (1926) and Chamberlin (1952) have used the name for two different species-groups neither of which includes *L. doriae*. *L. mediterraneus* from the south of France has long been recognized as a synonym of *L. doriae*. *L. doriae uccianensis* from Corsica was described as having the coxal pores oval, no more than twice as broad as long, and the spine VmC present on the 14th as well as the 15th leg (Verhoeff 1943): since both these features are found in one or other of the syntypes from Busalla the subspecies *uccianensis* should be disregarded. All the features separating *L. doriae* from *L. pilicornis* Newport are such as would be expected from its smaller size and, since the two forms are not known to be truly sympatric, Brölemann was probably correct in regarding them as no more than subspecifically distinct.

Pocock must first have named this form *L. busallae* but the name was never published.

14. *Lithobius birmanicus* Pocock

(Figs. 39 to 41)

Lithobius (*Archilithobius*) *birmanicus* Pocock, 1891b : 407.
Archilithobius birmanicus : Attems, 1914 : 97.
Lithobius (*Australobius*) *birmanicus* : Attems, 1938 : 345.
Archilithobius birmanicus var. *chandellensis* Larwood, 1949 : 136, figs. 3a–f.

TYPE LOCALITIES. Tharrawaddy and Palon, Burma.

MATERIAL EXAMINED. A jar labelled " *Lithobius* (*Arch.*) *birmanicus* (Pocock), 89.7.15.75, Tharrawaddy, E. W. Oates (c & p) " contains five males and four females, all mutilated, and one specimen so defective as to be unrecognizable.

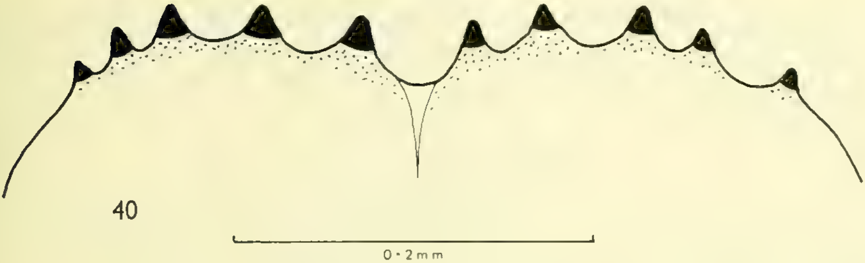
TYPE SPECIMEN. Pocock's description was based on a number of specimens from Tharrawaddy and Palon, Burma. No material from Palon has been found and the best preserved specimen from Tharrawaddy, a male 9·0 mm long, is here formally designated as the lectotype and has now been placed in a separate tube (Reg. no. 1889.7.15.75 (part)).

DESCRIPTION. *Size*: 8·0 to 9·5 mm long and 1·0 to 1·1 mm broad at T.10. *Colour*: dull yellow. *Shape*: fusiform; T.1 rather narrower than T.3; body broadest at T.8 or 10. *Head*: barely broader than long, about as broad as T.8 or 10. *Antennae*: almost half body-length, of 20 articles which become progressively more elongate distally. *Ocelli*: 1 + 3, 1 (Fig. 39) or 1 + 3, 2. *Prosternum*: with 4 + 4, 4 + 5, 5 + 5 or 5 + 6 teeth; lateral tooth or lateral two teeth smaller and placed more posteriorly than others; no lateral spine; lateral to lateral tooth the anterior border curves backwards without angulation (Fig. 40). *Tergites*: posterior angles of T.8 and 10 rounded, those of T.12 and 14 rounded or blunt; posterior borders of large tergites moderately emarginate; posterior angles of T.9, 11 and 13 obtusely rounded; intermediate tergite feebly emarginate posteriorly. *Coxal pores*: 2, 4, 4, 3; 3, 3, 4, 3; 3, 4, 4, 3; 3, 4, 4, 4 or 3, 5, 5, 4; circular; separated from one another by less than their own diameter. *Tarso-metatarsal articulations of anterior legs*: with, at most, a faint indication of an articulation. *15th leg*: missing in all specimens; according to Pocock the accessory apical claw is present. *Female gonopod*: coxa with two or three conical spurs set close to one another; when there are three the internal spur is much smaller than the others; claw tridentate (Fig. 41).

Spinulation of lectotype:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
13	—	m	amp	amp	m	a	—	amp	p	p
14	—	m	amp	amp	—	a	—	amp	p	—

15th coxa without lateral spine (VaC).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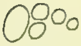
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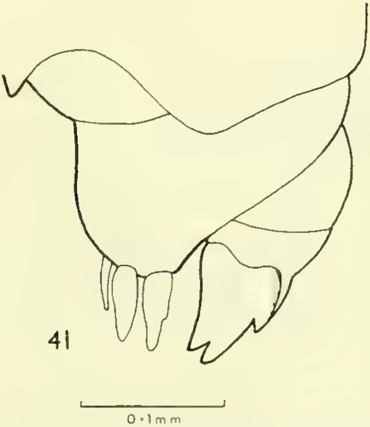
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FIGS. 39–41. *Lithobius birmanicus*. Fig. 39. Ocelli. Fig. 40. Dental margin of prosternum, ventral. Fig. 41. Left ♀ gonopod, ventral.

REMARKS. Attems (1914) and Larwood (1949) seem to have accepted the genus *Archilithobius* in Stuxberg's (1875) original sense (see p. 65) but *L. birmanicus* would not be included in *Archilithobius* as later emended by either Attems (1926) or Chamberlin (1952). *Australobius*, on the other hand, was erected by Chamberlin (1920b) to receive an Australian species (*A. scabrior* Chamberlin, probably introduced to Australia from the East Indies) and is characterized by antennae of only about 20 articles, relatively few large ocelli arranged in a compact mass, 3 + 3 or more prosternal teeth, frequent absence of the prosternal lateral spine and usually three or more spurs on the female gonopod. *L. birmanicus* and the next four species all seem to belong to *Australobius* which is distributed chiefly in India and south-east Asia.

Pocock described the 15th leg of *birmanicus* with only a single ventral spine each on the trochanter, prefemur and femur, but this reduced spinulation of the 15th leg is hardly credible when associated with the profuse ventral spinulation found on the 14th leg of the lectotype, and Pocock's description was probably based on an abnormal or regenerating leg. Larwood's naming of a new variety from India, *chandellensis*, characterized by three ventral spines on the prefemur and two on the femur of the 15th leg and agreeing with the lectotype in other respects (Larwood 1949) was not justified.

15. ***Lithobius feae*** Pocock

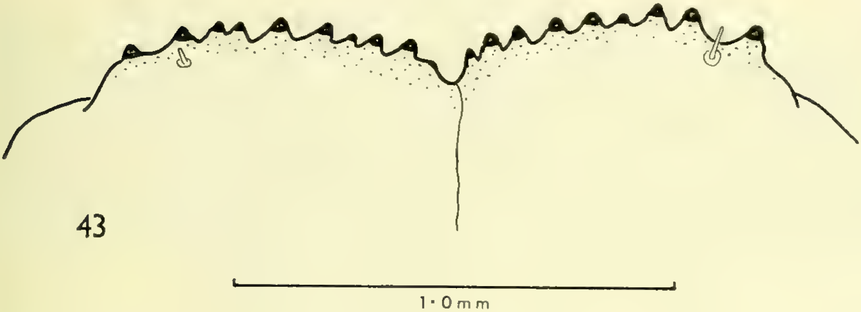
(Figs. 42 to 44)

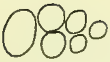
Lithobius feae Pocock, 1891b : 408; Attems, 1914 : 97; Silvestri, 1917 : 307, fig. I 1–13.
Lithobius (*Australobius*) *feae* : Attems, 1938 : 345; 1953 : 152.
Burmobius feae : Chamberlin, 1944b : 14.

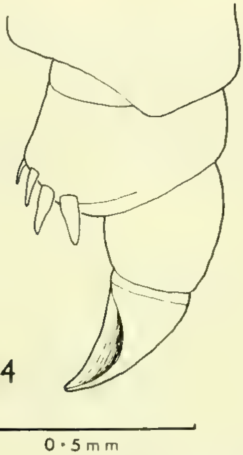
TYPE LOCALITY. Mount Mooleyit, Burma.

MATERIAL EXAMINED. A jar labelled "*Lithobius feae* Poc.? North Chin Hills (Upper Burma) E. Y. Watson, 93.11.12.3" contains a mutilated female. The single female on which Pocock's description was based was collected by Sig. L. Fea on Mount Mooleyit in Tenasserim (Lower Burma) so that the female in the British Museum (Natural History) cannot be the holotype : nor should it be selected as neotype because the North Chin Hills are too far from the type locality. However, there is no doubt as to its identity and as the only full description of *L. feae* in the literature, that of Silvestri (1917), was based on specimens from India, the female from the North Chin Hills is described below.

DESCRIPTION. *Size*: 20 mm long and 2·4 mm broad at T.10. *Colour*: destroyed by partial clearing. *Shape*: parallel-sided; T.1 broader than T.3, almost as broad as T.10; body broadest at T.8 and 10. *Head*: broader than long, as broad as T.10. *Antennae*: 7·5 mm long, of 20 very elongate articles, particularly those of the distal one-third which are two or three times longer than broad. *Ocelli*: 1 + 3, 2 (Fig. 42). *Prosternum*: with 9 + 9 teeth; lateral tooth set a little apart from the others and placed slightly more posteriorly, leaving a rather indefinite diastema; lateral spine minute, setiform, inserted immediately posterior or posteromedial to the diastema; since all the prosternal setae are missing the size of the lateral spine relative to that of the setae cannot be estimated but it is probably more slender and almost certainly much shorter than the largest of the setae; the whole dental margin projects slightly forwards from the rest of the prosternum (Fig. 43). *Tergites*: posterior angles of T.8 and 10 blunt, those of T.12 and 14 angulated; posterior borders of larger tergites broadly and increasingly emarginate from before backwards; posterior angles of T.7 with feeble broad projections, those of T.9, 11 and 13 with increasingly long rather blunt projections; intermediate tergite strongly emarginate. *Coxal pores*: 5, 6, 6, 6; oval or circular; separated from one another by about half their own diameter. *Tarso-metatarsal articulations of anterior legs*: fully developed and functional. *14th and 15th legs*: missing; according to Silvestri (1917) accessory apical claws are present on both. *Gonopod*: coxa with four conical spurs set fairly close to one another, the internal spur very small; claw simple (Fig. 44).







FIGS. 42–44. *Lithobius feae.* Fig. 42. Ocelli. Fig. 43. Dental margin of prosternum, ventral. Fig. 44. Left ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	amp	m	—	—	amp	a	a
2–7	—	—	p	amp	am	—	—	amp	ap	a
8	—	—	p	amp	am	—	—	amp	ap	ap
9–12	—	—	mp	amp	am	—	—	amp	ap	ap
13	—	m	amp	amp	am	a	—	amp	ap	ap

Lateral spine (VaC) present on 15th coxa only.

REMARKS. *Burmobius* was erected by Chamberlin (1944b) as a monotypic genus, characterized by the presence of a prosternal diastema in addition to the general features of *Australobius*, to receive *L. feae*. *Burmobius* is, therefore, equivalent to *Alloporodontius* Verhoeff which was erected as a subgenus of *Lithobius* to receive a number of Malayan species (Verhoeff 1937b) and was characterized in exactly the same way. But the prosternal diastema is not a striking feature in the specimen of *L. feae* from Upper Burma and was not noticed by Pocock in the original specimen. There is no evidence of Chamberlin having examined a specimen himself and he must have based *Burmobius* on Silvestri's illustration of the prosternum of an Indian specimen which shows a diastema between the four lateral and four medial teeth (Silvestri 1917 : fig. I 11). It may be that this intermediate position of the prosternal diastema characterizes an Indian subspecies of *L. feae* but it is more likely that the exact position and even the existence of a diastema are variable in this species.

16. ***Lithobius weberi*** Pocock

(Figs. 45 and 46)

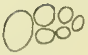
Lithobius (*Archilithobius*) *weberi* Pocock, 1894 : 310, Pl. 19 fig. 2.
Archilithobius javanicus : Attems, 1907 : 89 (non Pocock, 1894).
Archilithobius weberi : Attems, 1914 : 97.
Monotarsobius javanicus : Attems, 1914 : 97.
Tamulinus japanicus : Attems, 1927 : 244 (typ. error).
Lithobius (*Australobius*) *weberi* : Attems, 1938 : 345.
Lithobius (*Tamulinus*) *javanicus* : Attems, 1938 : 345.
Lithobius (*Australobius*) *javanicus* : Attems, 1953 : 151.

TYPE LOCALITIES. Manindjau and Mount Singalang, Sumatra.

MATERIAL EXAMINED. A jar labelled "*Lithobius javanicus* Pocock, *weberi* Pocock, type, 1896.10.6" contains a tube labelled "*Lithobius weberi* Pocock, type, Manindjau (Sumatra)". A male with the 13th, 14th and 15th legs missing.

TYPE SPECIMEN. Pocock's description was based on two males, one from Manindjau and one from Mount Singalang. The latter has not been found and the specimen from Manindjau is here formally designated as the lectotype (Reg. no. 1896.10.6.92).

DESCRIPTION OF LECTOTYPE. *Size*: 12 mm long and 1·6 mm broad at T.10. *Colour*: dull red. *Shape*: fusiform; T.1 as broad as T.3; body broadest at T.8 and 10. *Head*: broader than long, rather broader than T.5. *Antennae*: 4·0 mm long, of 20 slightly elongate articles. *Ocelli*: 1 + 3, 2 (Fig. 45). *Prosternum*: with 3 + 3 teeth all of much the same size; no lateral spine; lateral to lateral tooth the anterior border slopes gradually backwards without angulation (Fig. 46).



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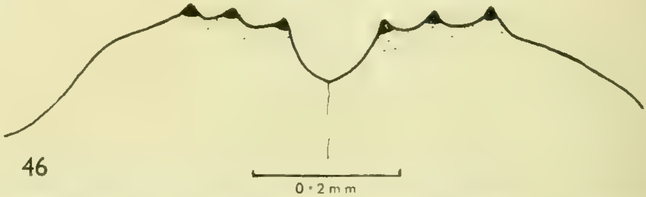

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FIGS. 45–46. *Lithobius weberi*. Fig. 45. Ocelli. Fig. 46. Dental margin of prosternum, ventral.

Tergites: large tergites with posterior angles rounded and posterior borders moderately emarginate; posterior angles of T.9, 11 and 13 squared; intermediate tergite feebly emarginate posteriorly. *Coxal pores*: 2, 3, 4, 3; circular; separated from one another by about their own diameter. *Tarso-metatarsal articulations of anterior legs*: with, at most, a faint indication of an articulation. *13th, 14th and 15th legs*: missing.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	p	a	—	—	—	amp	a	a
2–8	—	—	p	am	m	—	—	amp	ap	a
9–11	—	—	p	am	am	—	—	amp	p	a
12	—	—	p	m	am	—	—	amp	p	p

13th to 15th coxae without lateral spines (VaC); dorsal spine (DaC) present on 15th coxa only.

REMARKS. Attems (1907) described a single male from Buitenzorg (Java) which he identified as *Archilithobius javanicus* (Pocock) but there is no doubt that this specimen should have been referred to *L. weberi*: all Attems' subsequent references to, and brief descriptions of, *javanicus* were presumably based on this specimen as there is no evidence of his ever having seen an example of the true *L. javanicus*. His references to *weberi*, on the other hand, seem to have depended solely on Pocock's description and records.

As in the case of *L. birmanicus*, *L. weberi* would only be included in *Archilithobius* in Stuxberg's (1875) original sense. Attems (1914), finding that his specimen had fused tarsal articulations on the 1st to 13th legs, transferred "*javanicus*" (=*weberi*) to *Monotarsobius*, a genus erected by Verhoeff (1905) to receive those species with fused anterior tarsal articulations and only 19 to 22 antennal articles: at the same time Attems left *weberi* in *Archilithobius* on the assumption that these articulations are free in that species. He later (Attems 1927) transferred "*javanicus*" from *Monotarsobius* to *Tamulinus*, a genus he had himself erected (Attems 1926) to include those species excluded by Verhoeff's (1907) revised and more restricted definition of *Monotarsobius* by the possession of more than 2 + 2 prosternal teeth. He finally (Attems 1953) discarded *Tamulinus* as a useful division and transferred the species to *Australobius* (see p. 67) where it certainly belongs.

17. ***Lithobius javanicus*** Pocock

(Figs. 47 and 48)

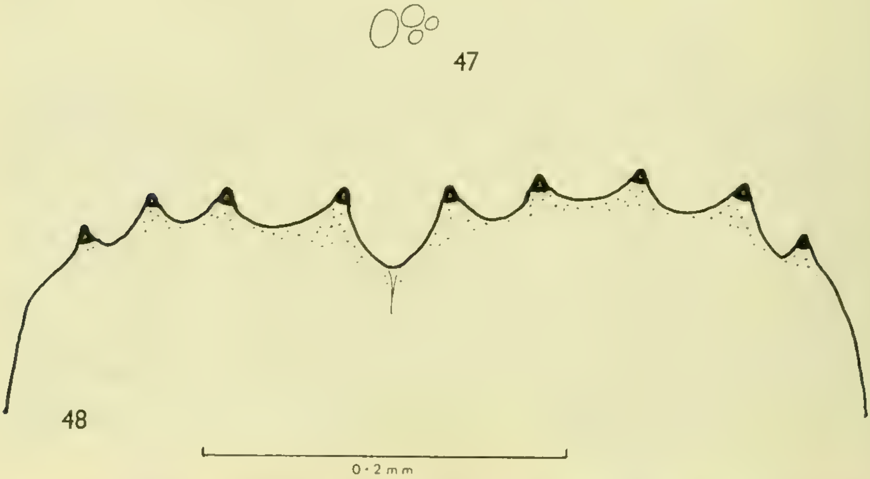
Lithobius (*Archilithobius*) *javanicus* Pocock, 1894: 311, Pl. 19 fig. 3.

TYPE LOCALITY. Tjibodas, Java.

MATERIAL EXAMINED. The jar labelled "*Lithobius javanicus* Pocock, *weberi* Pocock, type, 1896.10.6" contains a tube labelled "*Lithobius javanicus* Pocock, type, Tjibodas". A fairly well-preserved male.

TYPE SPECIMEN. Pocock's description is of a single male and the above specimen is the holotype (Reg. no. 1896.10.6.93).

DESCRIPTION OF HOLOTYPE. *Size*: 7·0 mm long and 0·9 mm broad at T.8. *Colour*: dull yellow. *Shape*: almost parallel-sided; T.1 as broad as T.3; body broadest at T.8. *Head*: barely broader than long, as broad as T.8. *Antennae*: 2·8 mm long, of 20 rather irregular articles. *Ocelli*: 1 + 2, 1 (Fig. 47). *Prosternum*: with 4 + 5 teeth; lateral tooth smaller and placed more posteriorly than others; no lateral spine; lateral to lateral tooth the anterior border slopes sharply backwards without angulation (Fig. 48). *Tergites*: posterior angles of T.8, 10, 12 and 14 blunt; posterior borders of large tergites very feebly emarginate; posterior angles of T.9, 11 and 13 rounded and very feebly projecting posteriorly; intermediate tergite feebly emarginate posteriorly. *Coxal pores*: 2, 2, 2, 2; circular; separated from one another by about their own diameter. *Tarso-metatarsal articulations of anterior legs*: quite distinct with a change in breadth of articles but no obvious flexion. *15th leg*: 2·5 mm long, not swollen or otherwise modified; accessory apical claw half the length of principal claw. *Male genitalia*: covered by genital sternite so that the specimen may be immature.



FIGS. 47–48. *Lithobius javanicus*. Fig. 47. Ocelli. Fig. 48. Dental margin of prosternum, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
14	—	m	amp	m	—	—	—	mp	p	—
15	—	m	amp	m	—	—	—	mp	—	—

Spinulation of anterior legs very deficient and difficult to interpret accurately.

REMARKS. *L. javanicus* may be no more than subspecifically distinct from *L. birmanicus* from which it can only be separated by means of the shape of the tergites and the form of the tarso-metatarsal articulations of the anterior legs: the other distinctive features may all be due to immaturity of the holotype and the true status of *javanicus* will only be decided when adults of both sexes have been examined. It should be regarded, provisionally, as a valid species.

18. ***Lithobius sculpturatus*** Pocock

(Figs. 49 to 51)

Lithobius sculpturatus Pocock, 1901 : 449; 1906 : 1041.
Monotarsobius ceylanicus Attems, 1909 : 21; 1914 : 97.
Archilithobius sculpturatus : Attems, 1914 : 97.
Tamulinus ceylanicus : Attems, 1927 : 244.
Lithobius (*Tamulinus*) *sculpturatus* : Attems, 1938 : 345.
Lithobius (*Tamulinus*) *ceylanicus* : Attems, 1938 : 345.
Lithobius (*Australobius*) *ceylanicus* : Attems, 1953 : 151.

TYPE LOCALITY. Madras, India.

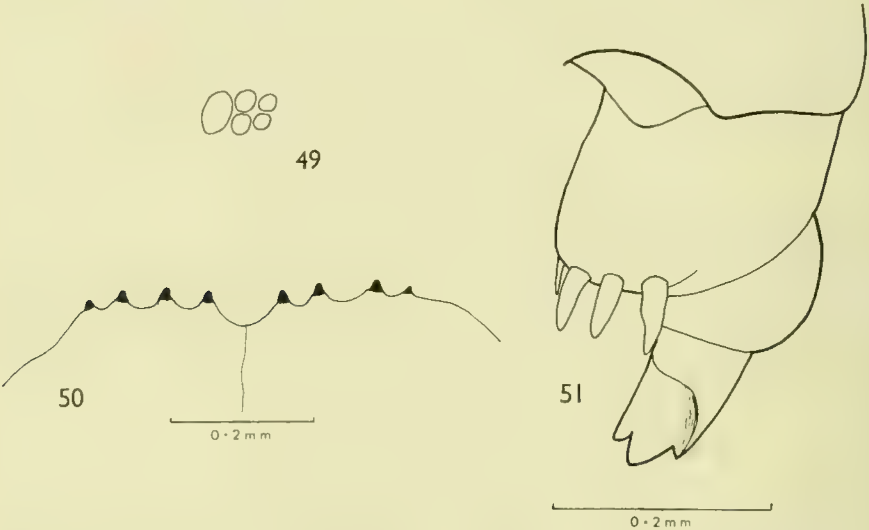
MATERIAL EXAMINED. A jar labelled "*Lithobius sculpturatus* Pocock, type, 1894.10.24.65–67" contains the following two tubes:

"Madras". A well-preserved female answering fairly well to Pocock's description (Reg. no. 1894.10.24.65).

"Kodaikanal". Two males differing from Pocock's description and belonging to another species to be described later in this paper (Reg. no. 1894.10.24.66–67).

TYPE SPECIMEN. Pocock implied that his description was based on a number of specimens from Kodaikanal (Palni Hills, southern India) and Madras, but he did not select any one specimen as type. The description was clearly based chiefly on the female from Madras which is conspecific with the specimens Pocock (1906) recorded as *L. sculpturatus* from the Maldive and Laccadive Islands, whereas the males from Kodaikanal are specifically distinct. The specimen from Madras is here formally designated as the lectotype (Reg. no. 1894.10.24.65).

DESCRIPTION OF LECTOTYPE. *Size*: 11·2 mm long and 1·25 mm broad at T.10. *Colour*: dark brown. *Shape*: feebly fusiform; T.1 broader than T.3; body broadest at T.8 and 10. *Head*: broader than long, as broad as T.10. *Antennae*: 3·6 mm long, of 20 fairly regular articles, mostly as broad as long. *Ocelli*: 1 + 2, 2 (Fig. 49). *Prosternum*: with 4 + 4 teeth; lateral tooth smaller and placed more posteriorly than others; no lateral spine; lateral to lateral tooth the anterior border slopes gradually backwards without angulation (Fig. 50). *Tergites*: posterior angles of T.8 and 10 rounded, those of T.12 and 14 blunt; posterior borders of large tergites moderately emarginate; posterior angles of T.9 obtuse, those of T.11 and 13 squared; intermediate tergite moderately emarginate posteriorly. *Coxal pores*: 4, 5, 5, 5 and 3, 5, 5, 4; circular; separated from one another by their own diameter. *Tarso-metatarsal articulations of anterior legs*: with, at most, a faint indication of an articulation. *15th leg*: 3·8 mm long; accessory apical claw half the length of principal claw. *Gonopod*: coxa with four conical spurs separated from one another at their insertions by rather less than their own breadth ; internal spur very small ; claw short, tridentate (Fig. 51).



FIGS. 49–51. *Lithobius sculpturatus*. Fig. 49. Ocelli. Fig. 50. Dental margin of prosternum, ventral. Fig. 51. Left ♀ gonopod, ventral.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	am	m	—	—	amp	a	a
2	—	—	p	am	m	—	—	amp	ap	a
3–8	—	—	p	amp	m	—	—	amp	ap	a
9	—	—	p	amp	m	—	—	amp	ap	ap
10	—	—	p	amp	am	—	—	amp	ap	ap
11	—	—	mp	amp	am	—	—	amp	ap	ap
12	—	—	mp	amp	am	—	—	amp	ap	p
13	—	—	amp	amp	a	—	—	amp	p	p
14	—	m	amp	amp	a	a	—	amp	p	p
15	a	m	amp	amp	a	a	—	amp	p	—

FURTHER SPECIMENS. Five males from the Maldive Islands and two females from the Laccadive Islands in the British Museum (Natural History) (Reg. no. 1952.12.11.73–78), on which Pocock (1906) reported, show general agreement with the lectotype but with the following variations : *Size*: 8·5 to 11 mm long. *Colour*: paler. *Antennae*: one male with only 19 articles. *Coxal pores*: 2, 3, 3, 3 ; 2, 3, 4, 3 ; 3, 3, 4, 3 or 2, 4, 4, 3. *14th and 15th legs*: slightly swollen in males. *Coxolateral spines* (*VaC*): present on 14th as well as 15th legs in one male. *Female gonopod*: with only three spurs in both specimens which may be immature.

REMARKS. Pocock overstated the number of ocelli in *L. sculpturatus* and also failed to record the single ventral tibial spine (VaT) on the 15th leg. Consequently Attems (1909) described a female from Pont de Galle, Ceylon, which clearly belonged to *sculpturatus*, as a new species, *Monotarsobius ceylanicus*, which he later designated as the type species of *Tamulinus* (Attems 1927). His generic classification of this species was much the same as for the specimen of *L. weberi* he identified as *javanicus* (see p. 71). Attems' references to the species by its correct name seem to have depended solely on Pocock's description. Like the last four species *L. sculpturatus* belongs to *Australobius*.

19. ***Lithobius shimensis*** Pocock

Lithobius shimensis Pocock, 1895b : 349.
Lithobius shinensis : Attems, 1914 : 97 (typ. error).
Lithobius (*Australobius*) *shimensis* : Attems, 1938 : 345 ; 1953 : 151.

TYPE LOCALITY. Tsu-Shima, Japan.

MATERIAL EXAMINED. A jar labelled "*Lithobius shimensis* Poc., Tsu-Shima, P. A. Holst, 91.11.15" contains two mutilated stadia agenitalis of *Bothropolys asperatus* (L. Koch, 1878).

TYPE SPECIMENS. The above two specimens are the syntypes (Reg. no. 1891. 11.15.2A).

DESCRIPTION. 7·0 mm and 5·5 mm long and answering to Murakami's (1958) description of the agenitalis II of *Bothropolys asperatus*.

REMARKS. Pocock, mistakenly, described adult female gonopods in *shimensis* and as the multiseriate coxal pores characteristic of *Bothropolys* and related genera only appear in the more advanced post-larval stadia it is not surprising that Attems (1938), who was guided solely by Pocock's description, should have referred this form to *Australobius* of which it possesses all the essential features. In fact *Australobius* does not seem to occur in Japan (Takakuwa 1939, 1941a).

20. ***Lithobius holstii*** Pocock

(Figs. 52 to 54)

Lithobius Holstii Pocock, 1895b : 349.
Monotarsobius crassipes Holstii : Attems, 1909 : 19 ; 1914 : 97 ; Takakuwa, 1941b : 292, fig. 1 ; Chamberlin and Wang, 1952 : 183.
Monotarsobius takakuwai Verhoeff, 1937a : 193.

TYPE LOCALITY. Ashinoju, Japan.

MATERIAL EXAMINED. A jar labelled "*Lithobius holstii* Pocock, Ashinoju (Japan), P. A. Holst, 91.5.16.23. Tsu-Shima (Japan), P. A. Holst, 91.11.15" contains the following two tubes :

"Ashinoju (Japan), P. A. Holst". A well-preserved female (Reg. no. 1891.5. 16.23).

"Tsu-Shima". A very mutilated male (Reg. no. 1891.11.15.2B).

TYPE SPECIMEN. Pocock made it quite clear that his description was based on the female from Ashinoju and that the specimen from Tsu-Shima was mutilated when he examined it. The former is therefore the holotype (Reg. no. 1891.5.16.23).

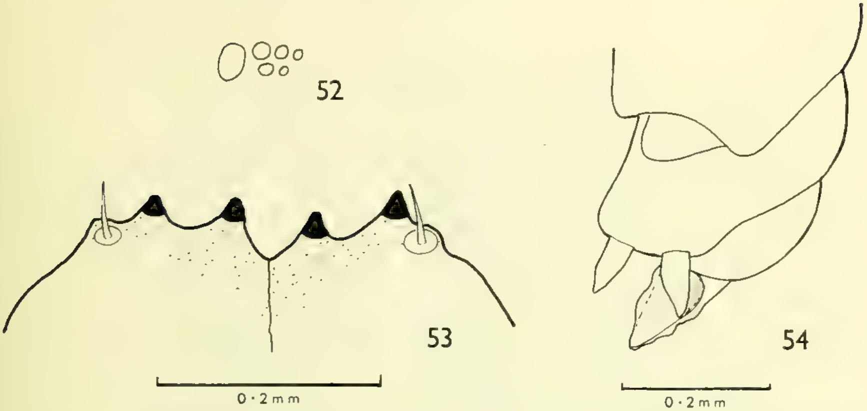
DESCRIPTION OF HOLOTYPE. *Size*: 8·0 mm long and 1·3 mm broad at T.10; the specimen is contracted and its length when alive must have been over 10 mm. *Colour*: yellow. *Shape*: fusiform; T.1 narrower than T.3; body broadest at T.10. *Head*: barely broader than long, as broad as T.3. *Antennae*: 3·2 mm long; the right antenna of 19 articles becoming increasingly elongate distally much as described by Verhoeff (1937a) in *Monotarsobius takakuwai*; the left antenna of 22 articles, all, including the terminal article, about as long as broad. *Ocelli*: 1 + 3, 2 (Fig. 52). *Prosternum*: with 2 + 2 teeth; lateral spine setiform, placed posterolateral to lateral tooth; immediately adjacent to the insertion of the spine is a distinct node; lateral to the node the anterior border curves backwards without angulation (Fig. 53). *Tergites*: large tergites with posterior angles rounded and posterior borders moderately emarginate; posterior angles of T.9, 11 and 13 rounded, not projecting; intermediate tergite broad and moderately emarginate posteriorly. *Coxal pores*: 3, 4, 4, 4; circular; separated from one another by about their own diameter. *Tarso-metatarsal articulations of anterior legs*: fused. *14th leg*: moderately swollen. *15th leg*: moderately swollen; 3·2 mm long; accessory apical claw three-fifths of length of principal claw. *Gonopod*: coxa with two conical spurs separated from one another at their insertions by about their own breadth and diverging from one another towards their apices; claw simple but with both internal and external ridges irregular (Fig. 54).

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	—	m	—	—	—	—	a
2	—	—	—	—	m	—	—	—	a	a
3–8	—	—	—	am	m	—	—	p	ap	ap
9–10	—	—	m	am	m	—	—	p	ap	ap
11	—	—	mp	am	m	—	—	p	ap	ap
12	—	—	mp	am	am	—	—	amp	ap	ap
13	—	—	amp	amp	am	—	—	amp	p	p
14	—	m	amp	am	m	a	—	amp	p	—
15	—	m	amp	am	—	a	—	amp	p	—

DaC very small on 14th and 15th legs.

REMARKS. The small number of antennal articles (19–22), 2 + 2 prosternal teeth, fused anterior tarsal articulations, and the absence of posterior tergal projections place *L. hostii* in *Monotarsobius* as redefined by Verhoeff (1907); but Attems (1909) was not justified in regarding this form as conspecific with *L.* (*Monotarsobius*) *crassipes* L. Koch from which it differs in many essential features. Pocock described the claw of the female gonopod as "obsoletely trifid" and this led Verhoeff (1937a) to name *Monotarsobius takakuwai* (from the neighbourhood of Tokyo)



FIGS. 52–54. *Lithobius holstii.* Fig. 52. Ocelli. Fig. 53. Dental margin of prosternum, ventral. Fig. 54. Left ♀ gonopod, ventral.

as a distinct species with a simple female genital claw. According to Takakuwa (1941b), who suggested the synonymy of *takakuwai* with *holstii*, the genital claw shows considerable variation in this species. One of the cotypes of *Monotarsobius takakuwai* Verhoeff in the British Museum (Natural History) (Reg. no. 1937.9.9.57), a male 11 mm long, is almost certainly conspecific with the holotype of *L. holstii.*

Lithobius palnis sp. nov.

(Figs. 55 to 58)

TYPE LOCALITY. Kodaikanal in the Palni Hills, India.

MATERIAL EXAMINED. The two syntypes of *Lithobius sculpturatus* Pocock from Kodaikanal (see p. 73).

TYPE SPECIMENS. Holotype adult male and paratype immature male. B.M. (N.H.) Reg. nos. 1894.10.24.66 (holotype); 1894.10.24.67 (paratype).

DESCRIPTION OF HOLOTYPE. *Size*: 10·8 mm long and 1·3 mm broad at T.10. *Colour*: brown. *Shape*: fusiform; T.1 rather narrower than T.3; body broadest at T.8 and 10. *Head*: broader than long, rather broader than T.5. *Antennae*: 3·8 mm long, of 20 articles; the basal article and numbers 3 to 7, 11 to 13 and 17 to 19 are as long as broad or slightly transverse; the second article and numbers 8 to 10 and 14 to 16 are distinctly elongate; the terminal article is very elongate. *Ocelli*: 1 + 2, 1 on right (Fig. 55); 1 + 3, 2 on left (Fig. 56). *Prosternum*: with 4 + 4 teeth; lateral tooth set a little apart from the others and placed slightly more posteriorly, leaving a distinct diastema; lateral spine setiform, inserted immediately posterior to the diastema; lateral to lateral tooth the anterior border slopes backwards without angulation (Fig. 57). *Tergites*: posterior angles of T.8 and 10 rounded, those of T.12 and 14 blunt; posterior borders of large tergites moderately emarginate; posterior angles of T.9, 11 and 13, rounded,

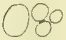
TABLE I

Nominal species	Date	Type locality	Designate type material	Validity and status
bermudensis	1893	Bermuda	Holotype	=*Lithobius sydneyensis* Pocock, 1891. SYN. NOV.
birmanicus	1891	Tharrawaddy, Burma	Lectotype	valid =*Archilithobius birmanicus* var. *chandellensis* Larwood, 1949. SYN. NOV.
decodontus	1895	Volcan de Acatenango, Guatemala	Holotype	valid
doriae	1890	Busalla, Italy	Lectotype	subspecies of *Lithobius pilicornis* Newport, 1844 =*Lithobius mediterraneus* Chalande, 1903 =*Lithobius doriae uccianensis* Verhoeff, 1943. SYN. NOV.
feae	1891	Mount Mooleyit, Burma	none	valid
godmani	1895	Amula, Guerrero, Mexico	Lectotype	valid
holstii	1895	Ashinoju, Japan	Holotype	valid =*Monotarsobius takakuwai* Verhoef, 1937
humberti	1895	Omilteme, Guerrero, Mexico	Lectotype	valid
javanicus	1894	Tjibodas, Java	Holotype	provisionally valid non *Archilithobius javanicus* : Attems, 1907
macroceros	1895	Omilteme, Guerrero, Mexico	Lectotype	valid =*Sotimpius multigranosus* Kraus, 1954 ?
persicus	1899	Seir, Persia	Holotype	valid
pontifex	1895	Amula, Guerrero, Mexico	Holotype	valid

TABLE 1 cont.

Nominal species	Date	Type locality	Designate type material	Validity and status
provocator	1891	Bermuda	Syntypes	=*Lithobius peregrinus* Latzel, 1880 =*Lithobius ethochaetus* Chamberlin, 1938. SYN. NOV.
salvini	1895	Omilteme, Guerrero, Mexico	Lectotype	valid
sculpturatus	1901	Madras, India	Lectotype	valid =*Monotarsobius ceylanicus* Attems, 1909. SYN. NOV.
shimensis	1895	Tsu-Shima, Japan	Syntypes	=*Bothropolys asperatus* (L. Koch, 1878). SYN. NOV.
stolli	1895	Volcan de Agua, Guatemala	Holotype	=*Lithobius castaneus* Newport, 1844. SYN. NOV.
sydneyensis	1891	Sydney, Australia	Lectotype	valid =*Lithobius bermudensis* Pocock, 1893 =*Lithobius araichensis* Brölemann, 1924. SYN. NOV. =*Walesobius excrescens* Attems, 1928. SYN. NOV. =*Lithobius platensis* Gervais : Silvestri, 1899 ? =*Chilebius coquimbo* Chamberlin, 1955 ? =*Andebius callao* Chamberlin, 1955 ?
vulcani	1895	Volcan de Agua, Guatemala	Holotype	valid =*Sotimpius zilchi* Kraus, 1954. SYN. NOV.
weberi	1894	Manindjau, Sumatra	Lectotype	valid =*Archilithobius javanicus* : Attems, 1907 (non Pocock, 1894)

those of T.11 and 13 very feebly projecting posteriorly (Fig. 58); the folds and tubercular elevations on the surface of the tergites noted by Chamberlin (1920b) in *Australobius scabrior* are present and most marked on T.10, 12 and 14, but they are no more pronounced than in the other species from India and south-east Asia; intermediate tergite moderately emarginate posteriorly. *Coxal pores*: 2, 3, 3, 3; circular; separated from one another by their own diameter. *Tarso-metatarsal articulations of anterior legs*: fully developed and functional. *14th leg*: slightly swollen. *15th leg*: slightly swollen; 3·8 mm long; accessory apical claw half the length of principal claw.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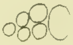
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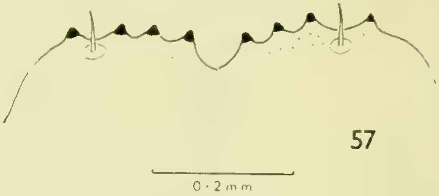
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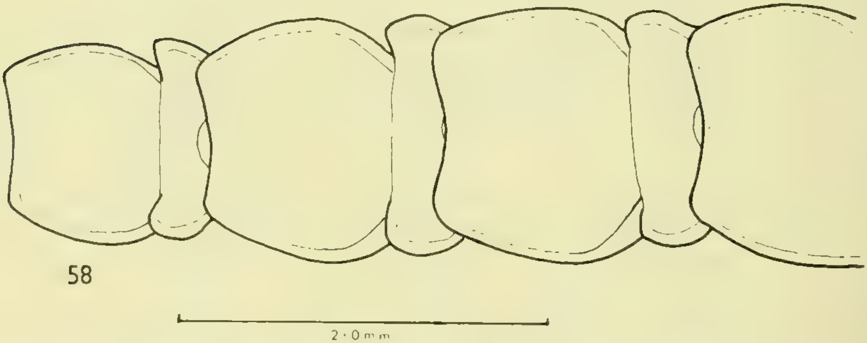
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FIGS. 55–58. *Lithobius palnis*. Fig. 55. Ocelli, right. Fig. 56. Ocelli, left. Fig. 57. Dental margin of prosternum, ventral. Fig. 58. 9th to 14th tergites, dorsal.

Spinulation:

	Ventral					Dorsal				
	C	t	P	F	T	C	t	P	F	T
1	—	—	—	—	—	—	—	p	a	a
2	—	—	p	a	—	—	—	mp	ap	a
3–4	—	—	p	a	m	—	—	amp	ap	a
5–6	—	—	p	am	m	—	—	amp	ap	a
7–9	—	—	—	am	m	—	—	amp	ap	a
10	—	—	—	am	m	—	—	amp	p	a
11	—	—	p	am	am	—	—	amp	p	a
12	—	—	p	am	am	(a)	—	amp	p	—
13	—	—	ap	amp	a(m)	a	—	amp	p	p
14	—	m	amp	amp	a	a	—	amp	p	—
15	—	m	amp	amp	a	a	—	amp	(p)	—

Letters in brackets indicate spines present on one side only.

DESCRIPTION OF PARATYPE. *Length*: 8·5 mm. *Antennae*: of 20 articles. *Ocelli*: 1 + 2, 2. *Prosternum*: with 4 + 3 teeth; lateral spine and diastema between the lateral two teeth on both sides. *Coxal pores*: 1, 2, 2, 2.

REMARKS. The presence of a prosternal diastema places the new species in *Alloporodontius* Verhoeff (=*Burmobius* Chamberlin) and it is close to *Lithobius* (*Alloporodontius*) *malayicus* Verhoeff from Johore, Malaysia (Verhoeff 1937b). It differs from *malayicus* in the absence of distinct triangular projections on T.9, 11 and 13 and in the position of the prosternal spine and diastema which, in *malayicus*, are between the intermediate two teeth. There is some doubt as to whether *Alloporodontius* should be retained as a division distinct from *Australobius* (see p. 69), and the exact status of *Australobius* remains uncertain until more is known of the lithobiid fauna of India and south-east Asia.

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FREELIVING MARINE NEMATODES FROM THE INDIAN OCEAN

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ZOOLOGY Vol. 25 No. 3
LONDON: 1973

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RICHARD M. WARWICK

Dove Marine Laboratory

Pp. 85–117 ; 14 *Text-figures*, 2 *Tables*

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FREELIVING MARINE NEMATODES FROM THE INDIAN OCEAN

By RICHARD M. WARWICK*

SYNOPSIS

Thirteen species of freeliving marine nematodes collected by the Royal Society's 1963 expedition to the South-east Arabian upwelling region of the Indian Ocean are described. Twelve of these species are new, all being referable to existing genera. *Didelta cobbi* sp. nov. is closest to *D. maculatum* Cobb, 1920 and is distinguished from this species by the form of the amphids, and possibly the arrangement of cephalic setae. *Procamacolaimus papillosus* sp. nov. is similar to *P. dolichostylum* Gerlach, 1953, but has shorter cephalic setae, no subventral buccal teeth and a differently shaped gubernaculum. *Sphaerolaimus crenellatus* sp. nov. is characterized by the posterior position of its amphids, a buttressed cephalic capsule and double-jointed spicules. *Siphonolaimus profundus* sp. nov. is apparently similar to *S. gladiator* Wieser, 1956, but differs from it in the setal arrangement on the head, the longer buccal spear and the presence of pre-cloacal supplements in the male. *Desmodora masira* sp. nov. is characterized by a short broad perforate cephalic capsule, small amphids, a weakly armed buccal cavity, a long tail and no male supplements. *Sabatieria alata* sp. nov. is very close to *S. furcillata* Wieser, 1954, but has a larger overall size, shorter cephalic setae, smaller amphids and a different spicule structure. *Hopperia muscatensis* sp. nov. is distinct from the type and only other species *H. massiliensis* Vitiello, 1969, in having longer cephalic setae, a shorter tail and differently shaped spicules. *Platycomopsis implicatus* sp. nov. is separated from its nearest relative *P. dimorphica* Mawson, 1956, in the setal arrangement on the head, the smaller amphids, the structure of the spicules and the position of the pre-cloacal supplement. *Synonchus alisonae* sp. nov. is characterized by the very long filiform tail and relatively long cephalic setae. Specimens of *Dayellus dayi* Inglis, 1964, conform exactly with the type, but are slightly smaller in many of the measurements. *Crenopharynx fringilla* sp. nov. is characterized by the combination of a long flagellate tail, spicules with no barbs or other modifications and a gubernaculum with pointed lateral pieces. *Mesacanthion southerni* sp. nov. is very closely related to *M. diplechma* Southern, 1914, but comparison with specimens of this latter species from the North Sea reveal differences of specific rank mainly concerning the copulatory apparatus of the male. *Mesacanthion arabium* sp. nov. is very characteristic: it has long spicules, a paired L-shaped gubernaculum with raised ridges at the distal end and unique accessory organs associated with the vulva in the female.

INTRODUCTION

DURING June and July 1963 the Royal Society mounted a cruise on the R.R.S. "Discovery" to the South-east Arabian upwelling region as part of the International Indian Ocean Expedition. Details of the work undertaken and stations sampled are given in the Cruise Report (Royal Society, 1963). Benthic samples were taken with a 0·1 m^2 Smith-McIntyre grab down to depths of 3500 m and undisturbed sediment hauls were subsampled with a corer for meiofauna analysis. These cores are very rich in meiofauna, particularly nematodes, and

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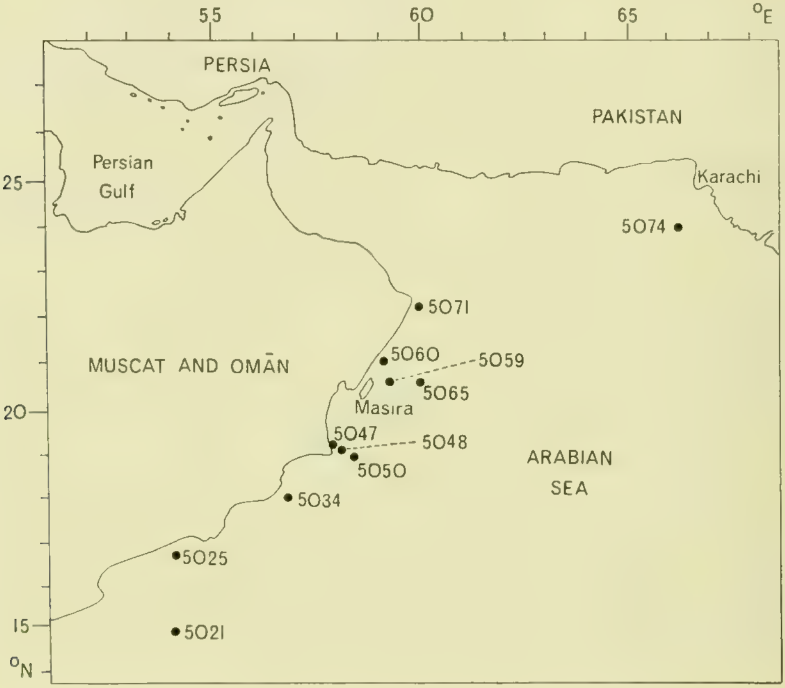
their extraction and analysis on a quantitative basis are proving very time consuming, so that completion of this work is not expected for some time. However, samples for macrofauna analysis passed through coarser sieves have been found to contain many new and interesting nematodes in the larger size range, and it is these which are described here. The sampling stations where the " macrofaunal " nematodes were found are listed in Table 1, together with information on the sediment types and the sieve size used. A map showing the positions of the stations is given in Fig. 1, and the species found at these stations are listed in Table 2.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PAKISTAN
Persian Gulf
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MUSCAT AND OMĀN
5060
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5065
Masira
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5050
ARABIAN SEA
5034
5025
5021

FIG. 1. Map showing positions of sampling stations.

Only species represented by at least one mature male specimen in good condition are described. Specimens have been mounted in glycerine for examination. Curved structures, e.g. spicules, are measured as the curve and not the chord, and head diameters are measured at the level of the anteriormost cephalic setae. Type-material is deposited at the British Museum (Natural History). When more than one specimen is available, descriptions are based on a syntypic series.

I am very grateful to Mr A. D. McIntyre of the Marine Laboratory, Aberdeen, for making this material available to me for study.

Table 1

Positions and other details of sampling stations

Date	Station no.	Position	Depth (m)	Sediment type	Sieve size
29.6.63	5021	14°55′N–53°55·4′E	2480	Greenish-grey mud	0·5 mm
30.6.63	5025	16°41′N–54°01·8′E	1030	Greenish fine sand	0·5 mm
5.7.63	5034	17°57·2′N–56°43·5′E	49	Fine sand	0·5 mm
10.7.63	5047	19°09·8′N–57°55·1′E	48	Fine muddy sand	0·5 mm
10.7.63	5048	19°03′N–58°02·8′E	120	Muddy sand	0·5 mm
10.7.63	5050	18°50′N–58°18·3′E	3147	Fine greyish-green mud	295 μ
15.7.63	5059	20°29·5′N–59°09·5′E	660	Greenish mud	295 μ
15.7.63	5060	21°03·5′N–59°04·1′E	50	Fine shelly sand	0·5 mm
16.7.63	5065	20°32·9′N–59°55·5′E	3500	Grey-green clay	295 μ
19.7.63	5071	22°12·9′N–59°54·3′E	1305	Greenish mud	295 μ
22.7.63	5074	23°57·0′N–66°08·0′E	182	Muddy sand with shells and some clay	0·5 mm

DESCRIPTIVE SECTION

Family **LINHOMOEIDAE**

Didelta cobbi sp. nov.

(Fig. 2)

Material studied. 1 ♂ (Holotype); B.M. (N.H.), Reg. No. 1972 : 354.

Representation. Station 5060.

De Man's Ratios.

	a	b	c	Body length (mm)
Male	106·00	19·91	9·81	4·24

Measurements (in mm). Male: Body breadth: 0·040. Oesophagus length: 0·213. Distance of nerve-ring from anterior: 0·079. Distance of excretory pore from anterior: 0·092. Length of longer cephalic setae: 0·014. Length of shorter cephalic setae: 0·003. Length of anterior cervical setae: 0·005. Length of posterior cervical setae: 0·010. Length of amphid + plaque: 0·015. Breadth of amphid + plaque: 0·0135. Tail length: 0·432. Cloacal diameter: 0·038. Spicule length: 0·051. Length of gubernacular apophysis: 0·029.

Description. The body is filiform, and of almost uniform width between the nerve-ring and cloaca. The cuticle is marked with fine transverse striations. The head bears a circle of ten cephalic setae, of which six are much longer than the remaining four. Between the cephalic setae and the amphids is a circle of four cervical setae, and posterior to the amphids six longer setae (Fig. 2c). The amphids are oval in outline, and are mounted on oval cuticularized plaques. The region where the amphidal nerve joins the centre of the amphid has an opaque granular appearance. The buccal cavity has an anterior thin-walled cup-shaped chamber separated from the posterior more heavily cuticularized chamber by a constriction. The oesophagus expands only slightly towards its base and is linked to the intestine by prominent cardia (Fig. 2b). The ventral excretory gland extends posteriorly to the level of the cardia.

TABLE 2

Distribution of species at the sampling stations

Station no.	Species	Numbers	
5021	*Synonchus alisonae* sp. nov.	4 ♂♂, 2 ♀♀, 9 juveniles	
5025	*Platycomopsis implicatus* sp. nov.	1 ♂	
5034	*Mesacanthion southerni* sp. nov.	1 ♂, 3 ♀♀	
	Mesacanthion arabium sp. nov.	4 ♂♂, 10 ♀♀	
	Viscosia sp.	1 ♀	
5047	*Dayellus dayi* Inglis, 1964	7 ♂♂, 5 ♀♀, 7 juveniles	
	Crenopharynx fringilla sp. nov.	7 ♂♂, 9 ♀♀, 12 juveniles	
	Mesacanthion southerni sp. nov.	5 ♂♂, 2 juveniles	
5048	*Theristus* sp.	3 ♂♂, 1 ♀	sample badly preserved; specimens in poor condition
	Cyatholaimidae sp.	2 ♀	
	Paranticoma sp.	1 ♀	
	Unidentifiable	6	
5050	*Siphonolaimus profundus* sp. nov.	4 ♂♂, 7 ♀♀, 2 juveniles	
	Desmodoridae sp.	1 ♀	
	Sabatieria alata sp. nov.	2 ♂♂, 5 ♀♀, 4 juveniles	
	Paramesacanthion sp.	1 ♀, 4 juveniles	
	Oncholaimidae spp.	1 ♂, 2 juveniles	
5059	*Desmodora masira* sp. nov.	6 ♂♂, 7 ♀♀	
	Sphaerolaimus crenellatus sp. nov.	7 ♂♂, 20 ♀♀	
5060	*Didelta cobbi* sp. nov.	1 ♂	
	Dayellus dayi Inglis, 1964	6 ♂♂, 13 ♀♀, 7 juveniles	
	Crenopharynx fringilla sp. nov.	2 ♂♂, 1 ♀	
	Oncholaimidae sp.	1 juvenile	
5065	*Steineria* sp.	1 ♀	
	Desmodora sp.	2 ♀♀	
	Paramesacanthion sp.	2 ♀♀, 1 juvenile	
5071	*Theristus* sp.	1 juvenile	
	Sabatieria sp.	1 juvenile	
	Hopperia muscatensis sp. nov.	1 ♂, 4 ♀♀	
	Oncholaimidae sp.	1 juvenile	
5074	*Procamacolaimus papillosus* sp. nov.	1 ♂	
	Crenopharynx sp.	1 juvenile	

The middle region of the body is devoid of setae. The tail is elongate with its distal two-thirds filiform. Numerous short setae are scattered ventrally immediately posterior to the cloaca, and longer setae are present at the junction of the conical and filiform sections of the tail (Fig. 2a).

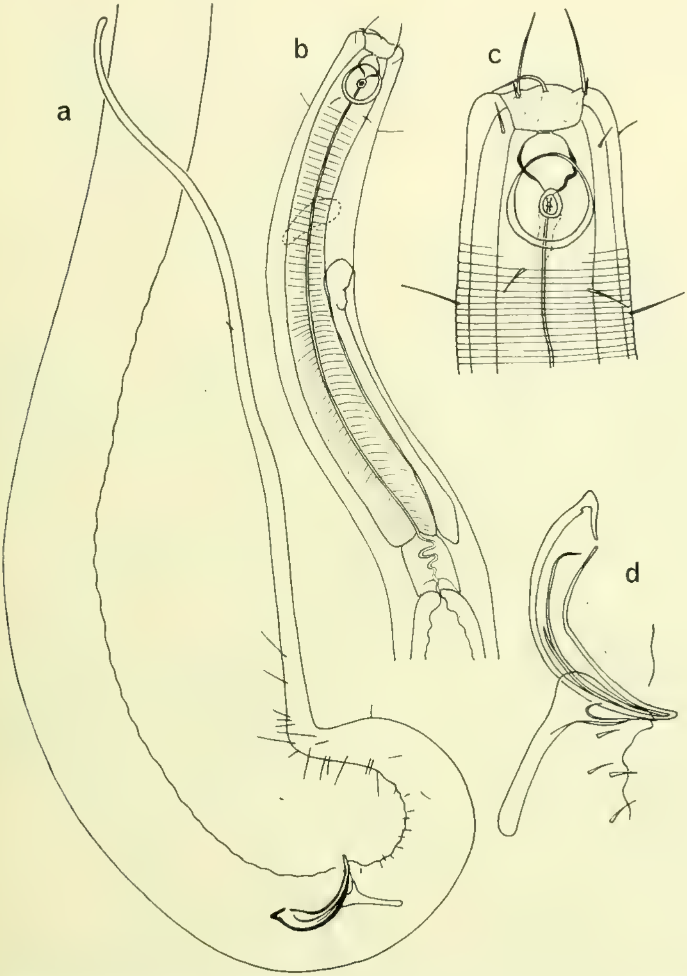

FIG. 2. *Didelta cobbi* sp. nov. a, Male tail. b, Anterior end of male. c, Lateral view of head. d, Lateral view of spicules and gubernaculum.

Male. The spicules are paired, equal and arcuate, with a median list. The gubernaculum bears long caudo-dorsal apophyses.

DISCUSSION. Currently four species are referable to this genus; *Didelta maculatum* Cobb, 1920, *D. scutata* Wieser, 1956, *D. cascudum* Gerlach, 1956, and *D. scutellata* Vitiello, 1969a. The last three of these species all have relatively short cephalic setae (less than 8 μ). The present species is separated from *D. maculatum* mainly by the shape of the amphids, which in the latter are much more elongate with the cuticular plate triangular in shape. The lateral cephalic setae are short in *D. maculatum* but appear to be long in *D. cobbi*. However, this feature is not at all clear in the holotype, since these setae seem to be rather bent.

Family **CAMACOLAIMIDAE**

Procamacolaimus papillosus sp. nov.

(Fig. 3)

MATERIAL STUDIED. 1 ♂ (Holotype); B.M. (N.H.), Reg. No. 1972 : 355.

REPRESENTATION. Station 5074.

DE MAN'S RATIOS.

	a	b	c	Body length (mm)
Male	105·45	9·16	29·00	3·48

MEASUREMENTS (in mm). Male: Body breadth: 0·033. Oesophagus length: 0·38. Excretory pore from anterior: 0·112. Proximal tip of ventral gland from base of oesophagus: 0·181. Head diameter: 0·012. Length of cephalic setae: 0·012. Amphid diameter: 0·0045. Tail length: 0·120. Cloacal diameter: 0·035. Spicule length: 0·051. Gubernaculum length: 0·027. Distance of pre-cloacal seta from cloaca: 0·023. Distance of posterior supplement from cloaca: 0·035. Distance of anterior supplement from cloaca: 0·28. Length of supplements: 0·021.

DESCRIPTION. The body is slender and elongate. The cuticle is marked throughout with rather coarse transverse striation. The mouth is surrounded by six rounded lips each bearing a short, stout, outwardly curving papilla. There are four relatively long cephalic setae. The buccal cavity is short and conical, and contains a solid styliform dorsal tooth opposed by a pair of pointed hollow subventral teeth. The amphids have a circular outline which is broken posteriorly for the exit of the amphidal nerve (Fig. 3b). The oesophagus is cylindrical, with no posterior swelling. The excretory pore is prominent and the ventral gland extends well beyond the base of the oesophagus. The tail is conical and bears two large rounded midventral papillae about half-way down its length. Smaller conical papillae are scattered generally over the surface of the tail (Fig. 3a).

Male. The spicules are paired, equal and arcuate. They expand in width gradually towards the proximal end, at which a rounded cephalization is set off by a constriction (Fig. 3c). Thin ventral spicular alae are present. The gubernaculum bears a strong rounded dorsal apophysis and triangular projections extending forwards on either side of the spicules. There is a stout pre-cloacal seta and nine strongly cuticularized pre-cloacal supplements. These are tubular, pointed distally and with their cephalate proximal ends again set off by a constriction.

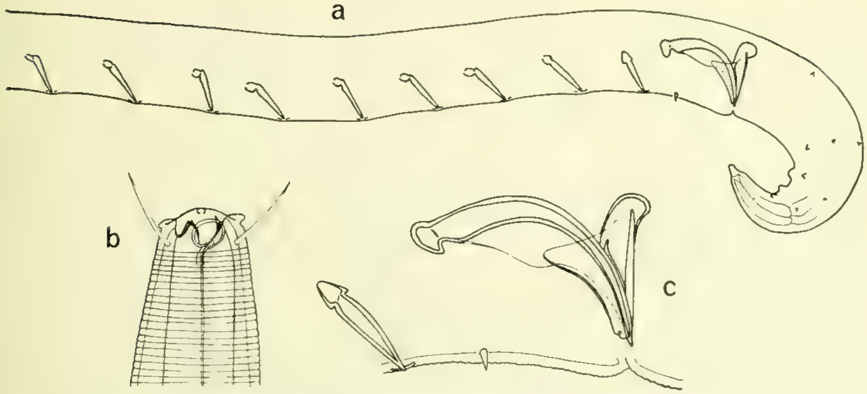

FIG. 3. *Procamacolaimus papillosus* sp. nov. a, Male tail. b, Lateral view of male head. c, Lateral view of spicules, gubernaculum and posterior supplement.

DISCUSSION. Of the four previously-described species *Procamacolaimus papillosus* sp. nov. is closest to *P. dolichostylum* Gerlach, 1953. The latter, however, has shorter cephalic setae, no subventral teeth in the buccal cavity and a differently-shaped gubernaculum.

Family SPHAEROLAIMIDAE

Sphaerolaimus crenellatus sp. nov.

(Fig. 4)

MATERIAL STUDIED. 5 ♂♂ and 5 ♀♀ (Syntypes); B.M. (N.H.), Reg. Nos. 1972 : 356–366 (3 ♂♂ and 2 ♀♀ measured below). Additional material: 2 ♂♂ and 15 ♀♀; B.M. (N.H.), Reg. Nos. 1972 : 367–382.

REPRESENTATION. Station 5059.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	21·47	5·53	9·22	–	2·49
	23·73	5·50	9·31	–	2·42
	25·27	5·47	9·40	–	2·35
Females	23·98	5·78	10·11	65·37	2·83
	27·11	5·76	10·24	62·57	2·765

MEASUREMENTS (in mm in order of body lengths). Males: Body breadth: 0·116; 0·102; 0·093. Oesophagus length: 0·45; 0·44; 0·43. Distance of nerve-ring from anterior: 0·175; 0·19; 0·18. Distance of excretory pore from anterior: 0·27; ? ; 0·26. Head diameter: 0·025; 0·028; 0·025. Length of cephalic setae: 0·004 + 0·003; 0·007 + 0·0045; 0·007 + 0·0045. Length of longest subcephalic setae: 0·020; 0·024; 0·024. Length of longest cervical setae: 0·0275; 0·029; 0·033.

Amphid diameter : 0·0125 ; 0·0125 ; 0·012. Body diameter at level of amphids : 0·062 ; 0·057 ; 0·056. Tail length : 0·27 ; 0·26 ; 0·25. Cloacal diameter : 0·072 ; 0·075 ; 0·071. Spicule length : 0·121 ; 0·132 ; 0·1125. Gubernaculum length : 0·049 ; 0·046 ; 0·045.

Females : Body breadth : 0·118 ; 0·102. Oesophagus length : 0·49 ; 0·48. Nerve-ring and excretory pore not visible. Head diameter : 0·033 ; 0·028. Length of cephalic setae : 0·0065 + 0·004 ; 0·007 + 0·004. Length of longest subcephalic setae : 0·025 ; 0·025. Length of longest cervical setae : 0·036 ; 0·037. Amphid diameter : 0·0095 ; 0·010. Body diameter at level of amphids : 0·063 ; 0·063. Tail length : 0·28 ; 0·27. Anal diameter : 0·065 ; 0·061. Distance of vulva from anterior : 1·85 ; 1·73.

Description. The cuticle bears fine transverse striations, and there is no sign of lateral differentiation. The mouth is surrounded by six lip-flaps which are triangular in *en-face* view (Fig. 4d). At the bases of the lips are six minute conical labial papillae. More posteriorly there is a circle of ten cephalic papillae ; the

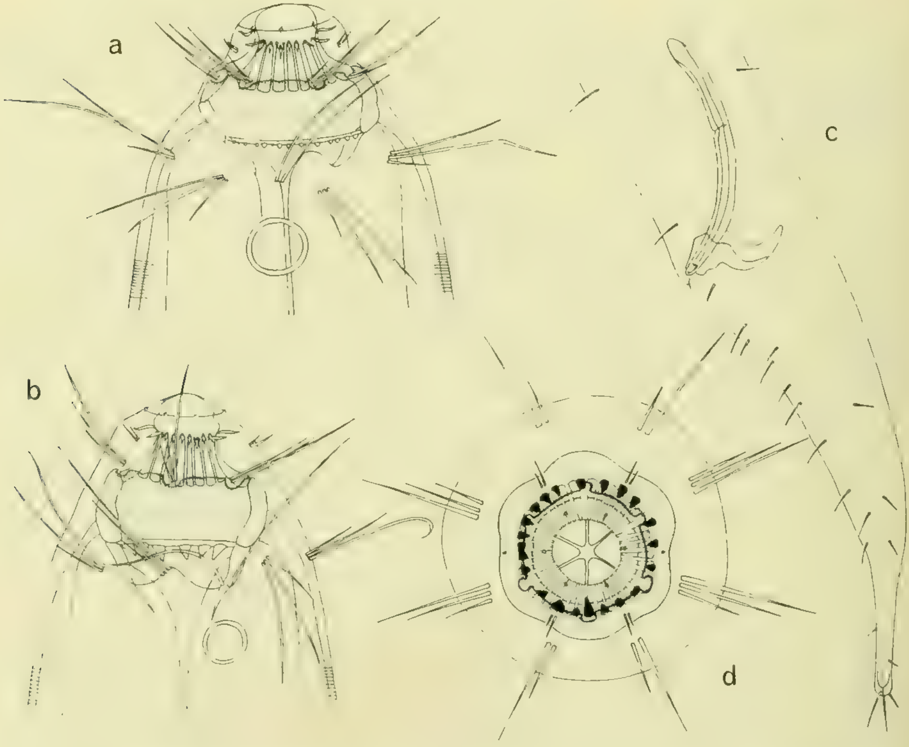

Fig. 4. *Sphaerolaimus crenellatus* sp. nov. a, Lateral view of male head. b, Lateral view of female head. c, Male tail. d, *En-face* view of head.

lateral ones are minute and conical and the submedian pairs longer, subequal and setiform. The subcephalic setae are arranged in eight groups with between two and four setae in each group. These setae are of different lengths, as shown in Figs. 4a, b and d. There are ten groups of cervical setae : eight triplets correspond in position with the cephalic setae and are of unequal length ; two pairs in the lateral positions just anterior to the amphids are of equal length. Eight files of longish setae (but not as long as the cervical setae) extend backwards from the head becoming progressively shorter until they disappear at about the level of the nerve-ring. Setae are scarce on the remainder of the body, becoming more numerous again on the tail, especially that of the male. The mouth opens into a small globular vestible (terminology of Inglis, 1961) which leads by a conical passage bordered by a leaf crown of forty cheilorhabdions to the heavily cuticularized globular buccal cavity. The anterior border of this cavity is indented with six rounded notches. At the posterior end of the buccal capsule there is a ring of buttresses similar to those described by Inglis (1961) for *S. anterides.* However, the buttresses are smaller than in this latter species, and triangular in shape. In both sexes the buttresses may be small and numerous (Fig. 4a) or less numerous and larger (Fig. 4b). They can only be counted accurately in *en-face* view (see 21 buttresses in Fig. 4d). Punctation and sclerotization of the buccal capsule are confined to its anterior half, and do not extend to the buttresses (cf. *S. anterides* where the buttresses are the only sclerotized parts of the buccal capsule). Posterior to the buccal capsule the oesophageal funnel is relatively shallow and bears no teeth, but the ventrolateral sectors of the oesophagus project into the funnel as two muscular lobes. The amphids are circular in outline and are situated wholly posterior to the buccal cavity. They are larger in the male than the female, and this is the only sexual dimorphism shown in the head of this species. The oesophagus is cylindrical with no posterior swelling, and has a thick cuticular lining. The intestine is very opaque. The tail is of similar shape in both sexes, the distal quarter being cylindrical (Fig. 4c).

Male. The spicules are paired and equal. They are divided in the middle by a fine suture, and distally each bears a laterally curving projection. The gubernaculum has a dorsally directed apophysis which for the most part is poorly cuticularized. Because of the opacity of the intestine, the testes are not visible.

Female. There is a single anterior ovary, but the opacity of the intestine again obscures details of its structure. There is no post-vulvar sac. The eggs are roughly spherical, a typical example measuring 0·112 × 0·099 mm. Of three gravid females, all contained only a single egg.

DISCUSSION. A key to the species known at that time is given by Wieser (1956), and Freudenhammer (1970) lists species described subsequently. The present species agrees with *S. gracilis* de Man, 1884, and *S. campbelli* Allgén, 1927, in having the amphids of both sexes wholly posterior to the buccal cavity. It is closest to *S. gracilis* on the basis of the relative lengths of the cephalic and subcephalic setae. Although *S. gracilis* is a very variable species (Lorenzen, 1969, for example describes three distinct forms), none of its varieties has a buttressed cephalic capsule or double-jointed spicules.

Family **SIPHONOLAIMIDAE**

Siphonolaimus profundus sp. nov.

(Fig. 5)

MATERIAL STUDIED. Material in general is rather fragmented. 2 complete ♂♂, 1 headless ♂ and 2 complete ♀♀ (Syntypes) ; B.M. (N.H.), Reg. Nos. 1972 : 383–386. Additional material : 1 complete ♂, 1 complete ♀, 1 complete juvenile, 7 head ends, 1 ♀ tail end, 1 juvenile tail end, 1 ♀ middle region ; B.M. (N.H.), Reg. Nos. 1972 : 387–389.

REPRESENTATION. Station 5050.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	85·43	19·29	41·24	–	5·98
	61·58	16·14	37·44	–	4.68
	–	–	–	–	headless
Females	72·83	21·61	34·36	71·19	6·70
	60·91	20·30	32·06	71·19	6·70

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·070 ; 0·076 ; –. Oesophagus length : 0·31 ; 0·29 ; –. Length of posterior oesophageal bulb : 0·085 ; 0·087 ; –. Breadth of posterior oesophageal bulb : 0·042 ; 0·041 ; –. Distance of nerve-ring from anterior : 0·149 ; 0·134 ; –. Head diameter : 0·012 ; 0·012 ; –. Length of cephalic setae : 0·008 + 0·0025 ; 0·008 + 0·0025 ; –. Length of buccal spear : 0·032 ; 0·032 ; –. Amphid width : 0·014 ; 0·014 ; –. Body diameter at level of amphids : 0·029 ; 0·028 ; –. Tail length : 0·145 ; 0·125 ; 0·153. Cloacal diameter : 0·046 ; 0·045 ; 0·046. Spicule length : 0·079 ; 0·083 ; 0·082. Gubernaculum length : 0·025 ; 0·027 ; 0·031.

Females : Body breadth : 0·092 ; 0·11. Oesophagus length : 0·31 ; 0·33. Length of posterior oesophageal bulb : 0·109 ; 0·105. Breadth of posterior oesophageal bulb : 0·044 ; 0·052. Distance of nerve-ring from anterior : ? ; 0·145. Head diameter : 0·0125 ; 0·012. Length of cephalic setae : 0·008 + 0·0025 ; 0·007 + 0·002. Length of buccal spear : 0·029 ; 0·036. Amphid width : 0·014 ; 0·014. Body diameter at level of amphids : 0·028 ; 0·028. Tail length : 0·195 ; 0·209. Anal diameter : 0·050 ; 0·050. Distance of vulva from anterior : 4·77 ; 4·77. Egg length × breadth : 0·29 × 0·08 ; 0·265 × 0·08.

DESCRIPTION. The cuticle is marked with fine transverse striations. The head bears a circle of ten cephalic setae, of which four are longer and stouter than the remaining six. Two sets of four short setae are positioned just anterior to and just posterior to the amphids. Setae are scarce on the remainder of the body. The amphids are basically circular in outline, but their margin is considerably expanded along the posterior edge (Fig. 5a), where the amphidal nerve exits. The buccal cavity is typical of the genus, containing a long cuticularized axial spear. The oesophagus is expanded posteriorly into an elongate bulb. The intestine is full of small opaque black granules, as in many other species in the genus. The tail is conical in both sexes, and in the male bears two files of short subventral setae (Fig. 5c).

Male. The male tail is often tightly coiled, and the spicules in all specimens are extruded. The spicules are paired, equal and arcuate. They have a central list which occupies their proximal two-thirds. The gubernaculum has strongly

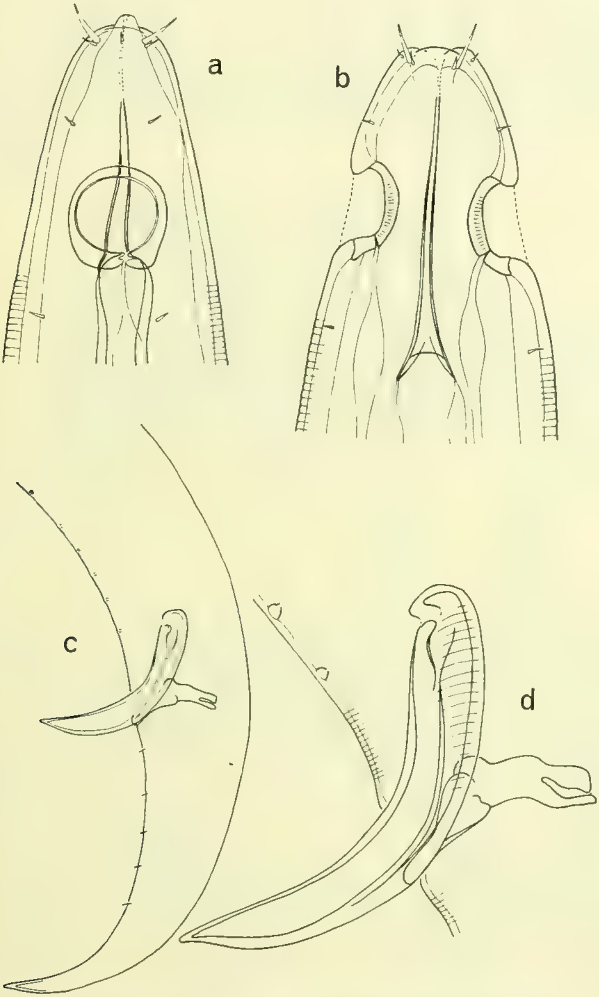

Fig. 5. *Siphonolaimus profundus* sp. nov. a, Lateral view of male head. b, Dorsal view of male head. c, Male tail. d, Lateral view of spicules, gubernaculum and posterior two supplements.

developed dorsal apophyses (Fig. 5d). When the tail is coiled the cuticle for some distance in front of, and a short distance behind, the cloaca is thrown into folds. This obscures the arrangement of the supplements. In the uncoiled tail a series of distinct pre-cloacal supplements is visible. These are small, cup-shaped and weakly cuticularized. They number about 32, are more or less equally spaced, and extend about 5·7 tail lengths in front of the cloaca.

Female. The female has a single anterior outstretched ovary. The uterus contains a single large and elongate egg in all specimens examined.

DISCUSSION. In the form of the amphids, tail and spicules this species appears to be very similar to *S. gladiator* Wieser, 1956. However, this species is much smaller, has only four cephalic setae, a different arrangement of cervical setae, a shorter spear and no supplements.

Family **DESMODORIDAE**

Desmodora masira sp. nov.

(Fig. 6)

MATERIAL STUDIED. 3 ♂♂ and 3 ♀♀ (Syntypes) ; B.M. (N.H.), Reg. Nos. 1972 : 390–395 (2 ♂♂ and 2 ♀♀ measured below). Additional material : 3 ♂♂, 4 ♀♀ and one head end ; B.M. (N.H.), Reg. Nos. 1972 : 396–403.

REPRESENTATION. Station 5059.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	57·40	14·64	10·63	–	2·87
	56·98	14·25	10·98	–	3·02
Females	45·42	14·73	10·55	38·84	3·27
	40·26	14·10	10·03	41·83	3·06

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·050 ; 0·053. Oesophagus length : 0·196 ; 0·212. Length × breadth of posterior oesophageal bulb : 0·061 × 0·040 ; 0·064 × 0·045. Head diameter (at level of four long cephalic setae) : 0·032 ; 0·031. Amphid diameter : 0·0075 ; 0·0085. Length of four long cephalic setae : 0·008 ; 0·007. Tail length : 0·27 ; 0·275. Cloacal diameter : 0·038 ; 0·042. Spicule length : 0·063 ; 0·068. Gubernaculum length : 0·019 ; 0·023.

Females : Body breadth : 0·072 ; 0·076. Oesophagus length : 0·222 ; 0·217. Length × breadth of posterior oesophageal bulb : 0·069 × 0·043 ; 0·072 × 0·047. Head diameter : 0·031 ; 0·033. Amphid diameter : 0·008 ; 0·008. Length of cephalic setae : 0·0075 ; 0·007. Tail length : 0·31 ; 0·305. Anal diameter : 0·031 ; 0·033. Distance of vulva from anterior : 1·27 ; 1·28. Egg length × breadth : 0·114 × 0·052 ; –.

DESCRIPTION. The cuticle is marked with distinct transverse striations between the posterior edge of the cephalic capsule and a short distance from the tail tip. The head is bluntly rounded. There are six very short conical cephalic setae anterior to the cephalic capsule, and four longer cephalic setae at the anterior border of the capsule. The capsule itself is made of very thick cuticle, and is perforated all over with conspicuous pores. There are small patches of rather opaque sclerotization at the bases of the cephalic setae. The capsule is relatively short, its width being more than twice its height. The amphids are small, and describe a spiral of two turns (Fig. 6a). The buccal cavity is quite small and contains a rather indistinct small pointed dorsal tooth. Six files of short setae extend down the length of the body, these being most numerous in the cervical region and on the male tail. The oesophagus is swollen posteriorly into a pyriform bulb, the cuticular lining of which shows no special thickening. The nerve-ring encircles the oesophagus immediately anterior to this bulb. The tail is relatively long and is evenly tapered throughout its length. The cuticle on the tail tip is clear and unmarked (Fig. 6c).

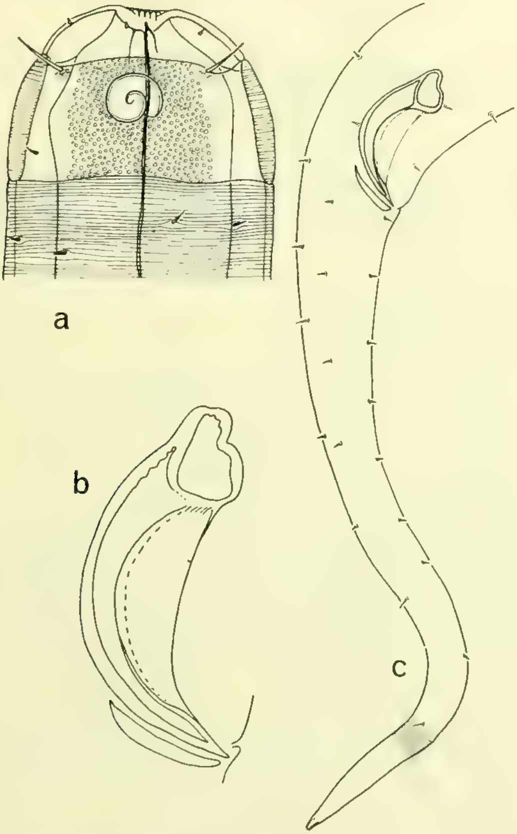

FIG. 6. *Desmodora masira* sp. nov. a, Lateral view of male head. b, Lateral view of spicules and gubernaculum. c, Male tail.

Male. The spicules are paired, equal and arcuate. They are strongly cephalated proximally and pointed distally, with ventral alae (Fig. 6b). The gubernaculum is small and plate-like. There are no pre- or post-cloacal supplements.

Female. The ovaries are paired, symmetrical, opposed and reflexed. The eggs are quite large when only a few are present but there may be up to six in each uterus, and they appear smaller when squashed together. The measurement given above represents the maximum size.

DISCUSSION. Gerlach (1963) has extensively revised the genus *Desmodora.* The present species belongs to group IA in Gerlach's subgeneric key, and can probably be ascribed to the subgenus *Desmodora*, although the cephalic capsule is shorter than in other members of the subgenus. *D. masira* sp. nov. is characterized by the combination of a short broad perforate cephalic capsule, small amphids, a weakly armed buccal cavity, a relatively long tail and the absence of supplements in the male.

Family **COMESOMATIDAE**

Sabatieria alata sp. nov.

(Fig. 7)

MATERIAL STUDIED. 2 ♂♂ and 2 ♀♀ (Syntypes); B.M. (N.H.), Reg. Nos. 1972: 404–407. Additional material: 3 ♀♀ and 4 juveniles; B.M. (N.H.), Reg. Nos. 1972: 408–414.

REPRESENTATION. Station 5050.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	52·79	10·06	11·71	–	3·22
	36·99	9·90	11·37	–	3·07
Females	42·71	9·34	10·31	48·16	2·99
	36·10	8·69	10·30	49·28	2·78

MEASUREMENTS (in mm in order of body lengths). Males: Body breadth: 0·061; 0·083. Oesophagus length: 0·32; 0·31. Distance of nerve-ring from anterior: ?; 0·148. Head diameter: 0·016; 0·0175. Length of longer cephalic setae: 0·005; 0·0055. Amphid diameter: 0·010; 0·011. Body diameter at level of amphids: 0·018; 0·019. Tail length: 0·275; 0·27. Cloacal diameter: 0·051; 0·050. Spicule length: 0·082; 0·090. Gubernaculum length: 0·030; 0·036.

Females: Body breadth: 0·070; 0·077. Oesophagus length: 0·32; 0·32. Distance of nerve-ring from anterior: 0·155; 0·149. Head diameter: 0·019; 0·020. Length of longer cephalic setae: 0·0055; 0·005. Amphid diameter: 0·011; 0·010. Body diameter at level of amphids: 0·020; 0·022. Tail length: 0·29; 0·27. Anal diameter: 0·051; 0·051. Distance of vulva from anterior: 1·44; 1·37.

DESCRIPTION. The cuticle is marked with transverse rows of fine punctations. Laterally the punctations are larger, wider spaced and more irregularly arranged. The mouth is surrounded by six rounded lips each bearing a small conical labial papilla. Anteriorly there are six short conical cephalic setae, and more posteriorly four longer ones. Cervical setae are short and scattered. The amphids of the male describe a spiral of 3·0–3·2 turns, and those of the female 2·8–3·0 turns. The buccal cavity is simply cup-shaped, and bears no armament (Fig. 7a). The basal third of the oesophagus is slightly expanded, but there is no distinct bulb. The tail is relatively long, with its distal half filiform (Fig. 7b).

Male. The spicules are paired, equal and arcuate. The proximal ends are only slightly cephalate, and from each a median list extends one-third of the way down the length of the spicule. When the spicules are protruded it can be seen that their ventral alae are produced into subterminal pointed projections near the distal ends (Fig. 7c). The gubernaculum bears a pair of pointed lateral projections in

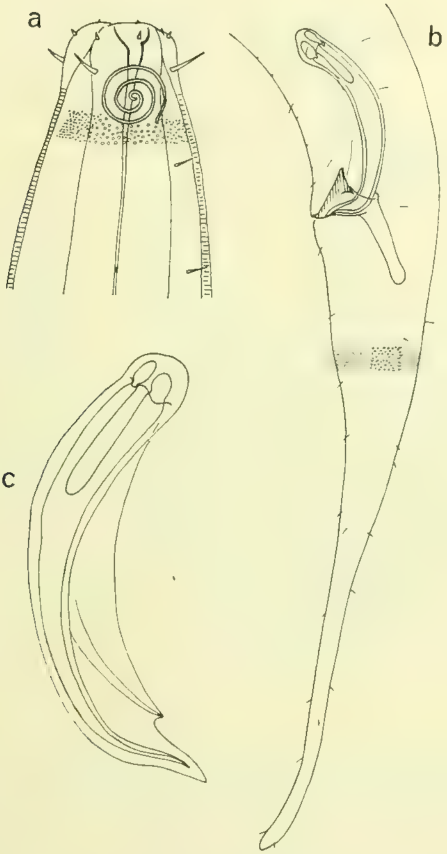

FIG. 7. *Sabatieria alata* sp. nov. a, Lateral view of female head. b, Male tail. c, Lateral view of spicule.

addition to the long round-ended caudodorsal apophyses. There are about 21 very small and inconspicuous pre-cloacal supplements. These consist of simple pores in the cuticle which are rather widely spaced, the anteriormost being approximately two tail lengths in front of the cloaca.

Female. The ovaries are paired, equal, opposed and reflexed.

DISCUSSION. This species is very close to *S. furcillata* Wieser, 1954. However, Wieser's species is smaller, has longer cephalic setae and relatively larger amphids. The spicules of the two species are differently shaped, the median list in *S. furcillata* being half the length of the spicule. Since species within the genus *Sabatieria* are generally separated on small but distinct characters, it is preferable to keep these two species distinct although the differences between them are quite small.

Hopperia muscatensis sp. nov.

(Fig. 8)

MATERIAL STUDIED. 1 ♂ and 4 ♀♀ (Syntypes); B.M. (N.H.), Reg. Nos. 1972: 415–419 (only 1 ♂ and 2 ♀♀ measured below).

REPRESENTATION. Station 5071.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Male	43·72	8·74	14·14	–	1·88
Females	35·63	9·12	13·99	46·49	2·28
	31·13	8·50	12·85	45·70	2·21

MEASUREMENTS (in mm in order of body lengths). Male: Body breadth: 0·043. Oesophagus length: 0·215. Distance of nerve-ring from anterior: 0·111. Distance of excretory pore from anterior: 0·129. Head diameter: 0·012. Length of longer cephalic setae: 0·005. Amphid width: 0·010. Body diameter at level of amphids: 0·014. Tail length: 0·133. Cloacal diameter: 0·034. Spicule length: 0·087. Length of gubernacular apophysis: 0·032.

Females: Body breadth: 0·064; 0·071. Oesophagus length: 0·25; 0·26. Distance of nerve-ring from anterior: 0·129; ?. Distance of excretory pore from anterior: 0·142; ?. Head diameter: 0·012; 0·013. Length of longer cephalic setae: 0·007; 0·005. Amphid width: 0·009; 0·008. Body diameter at level of amphids: 0·014; 0·017. Tail length: 0·163; 0·172. Anal diameter: 0·041; 0·042. Distance of vulva from anterior: 1·06; 1·01. Egg length × breadth: –; 0·057 × 0·050.

DESCRIPTION. The cuticle is marked by transverse rows of fine punctations. Lateral differentiation consisting of larger and more widely spaced punctations commences a short distance posterior to the amphids and terminates at the base of the conical portion of the tail. Very coarse lateral dots are present in the cloacal region of the male. The head bears two circles of six labial and six cephalic conical papillae. More posteriorly are four longer cephalic setae. The amphids describe a spiral of 3·1–3·2 turns and are slightly longer than wide. The mouth opens into a small globular cavity, the walls of which appear to be supported by fine cuticularized rods. More posteriorly the buccal cavity consists of a long heavily cuticularized tube, at the anterior end of which are three (one dorsal and two subventral) solid triangular teeth (Fig. 8a). A few very short scattered cervical, caudal and pre-anal setae are present, these being particularly numerous on the male tail. The oesophagus is swollen slightly towards its base, but there is no distinct bulb. Small cardia link the oesophagus with the intestine. The tail is relatively short, with its distal third filiform. It has a slightly swollen and rounded tip bearing a pair of short terminal setae (Fig. 8b).

Male. The spicules are paired, equal and arcuate. The proximal third contains a median list, and there is a dorsal opening near the proximal tip. Each spicule bears a small tooth ventrally near the distal end (Fig. 8c). The gubernaculum has long slightly curved apophyses with rounded ends. Pre-cloacal supplements in the form of fine cuticular pores are present, but are very indistinct and cannot be enumerated with certainty.

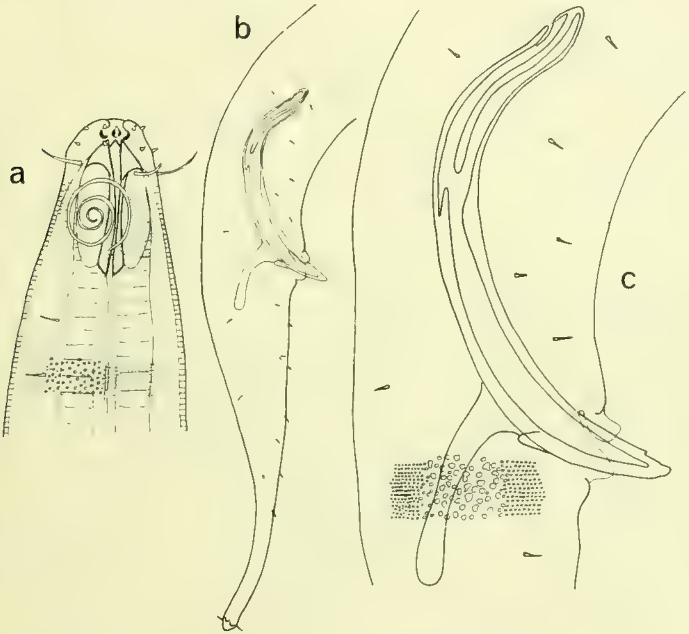

FIG. 8. *Hopperia muscatensis* sp. nov. a, Lateral view of male head. b, Male tail. c, Lateral view of cloacal region of male.

Female. The ovaries are paired and opposed, but do not appear to be reflexed. The posterior ovary is a little longer than the anterior. In the only female which is gravid, the anterior uterus contains two eggs and the posterior uterus three.

DISCUSSION. *Hopperia muscatensis* differs from the type and only other species, *H. massiliensis* Vitiello, 1969, on several points, the chief of which are the longer cephalic setae, the different form of the spicules and the much shorter tail.

Family **LEPTOSOMATIDAE**

Platycomopsis implicatus sp. nov.

(Fig. 9)

MATERIAL STUDIED. 1 ♂ (Holotype); B.M. (N.H.), Reg. No. 1972 : 420.

REPRESENTATION. Station 5025.

DE MAN'S RATIOS.

	a	b	c	Body length (mm)
Male	63·61	5·84	48·93	11·45

MEASUREMENTS (in mm). Male: Body breadth: 0·18. Oesophagus length: 1·96. Distance of nerve-ring from anterior: 0·47. Head diameter: 0·035. Length of cephalic setae: 0·025 + 0·015. Length of longest cervical setae: 0·027. Width of amphidal opening: 0·012. Tail length: 0·234. Cloacal diameter: 0·105. Spicule length: 0·095. Distance of supplement anterior to cloaca: 0·203.

DESCRIPTION. The cuticle is smooth. The mouth is surrounded by three low rounded lips, each bearing a pair of short conical labial papillae. There are ten cephalic setae, six being longer than the remaining four. Just posterior to the amphids on the lateral surfaces of the body are several transverse rows of long stout cervical setae. On the left side from anterior to posterior there are four rows numbering six, three, two and two setae respectively. On the right side there are only three rows, numbering four, three and one setae (Figs. 9a and b). On the dorsal surface there are similarly two rows of four and two long setae, but ventrally there are only two very short conical setae and there is no indication that any longer setae have been lost. More posteriorly there are a few very short setae in the cervical region and on the tail tip, but the middle region of the body is naked. The cephalic capsule is very weakly developed. It takes the form of a narrow band of sclerotization of the inner cuticle surrounding the head, and is only visible in optical section where its curves round the sides of the head. There is virtually no buccal cavity; the mouth opening merges imperceptibly into the lumen of the oesophagus. The amphids are pocket-like, with transverse oval openings. The oesophagus is cylindrical. The tail is conical but has a short cylindrical tip. There is no spinerette and no caudal glands are visible (Fig. 9c).

Male. The spicules are paired, equal and straight with a rather complex folded structure (Fig. 9d). They have funnel-shaped openings at their proximal ends. The gubernaculum is also complex and is folded into a pair of tubes surrounding each spicule. The pre-cloacal supplement comprises a simple mid-ventral papilla pierced by a fine pore from which a duct leads to the interior.

DISCUSSION. Mawson (1956) provides a useful key to the species of this genus. *Platycomopsis implicatus* appears to be closest to *P. dimorphica* Mawson, 1956.

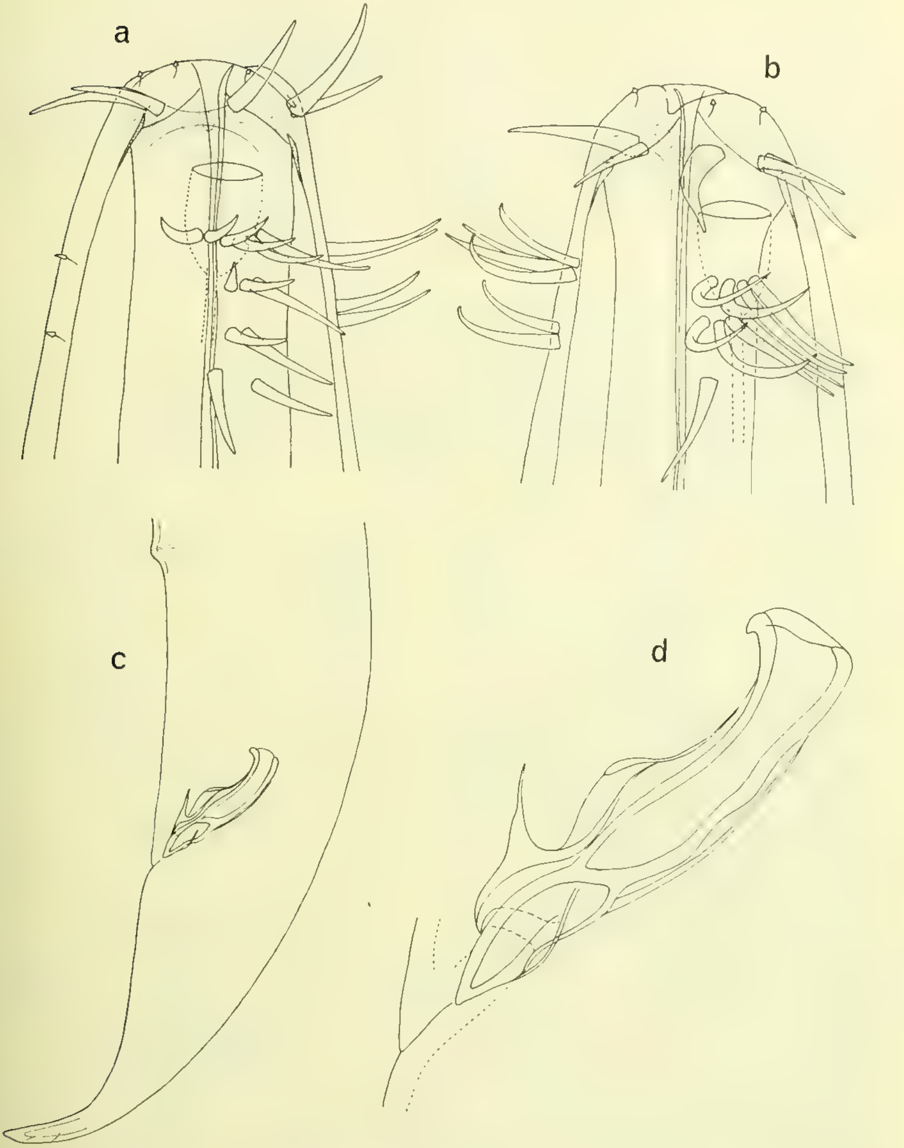

FIG. 9. *Platycomopsis implicatus* sp. nov. a, Male head from left side. b, Male head from right side. c, Male tail. d, Lateral view of spicules and gubernaculum.

This latter species has single long dorsal and ventral cervical setae and the post-amphidal setae are less numerous than in the present species. The aperture of the amphids seems to be very much wider in Mawson's species. She found it difficult to discern the structure of the spicules, because of the thickness of the tail, but in her drawing she shows the spicule narrowing abruptly near the proximal end, and not widening into a funnel-shaped opening. A final point of distinction between the two species is the position of the pre-cloacal supplement. In *P. dimorphica* it is situated less than one spicule length in front of the cloaca, whereas in *P. implicatus* the corresponding distance is more than twice the spicule length.

Synonchus alisonae sp. nov.

(Fig. 10)

MATERIAL STUDIED. 3 ♂♂ and 2 ♀♀ (Syntypes); B.M. (N.H.), Reg. Nos. 1972 : 421–425. Additional material: 1 ♂ and 9 juveniles, one of which is beheaded for an *en-face* preparation; B.M. (N.H.), Reg. Nos. 1972 : 426–435.

REPRESENTATION. Station 5021.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	58·50	7·18	27·86	–	11·70
	47·68	6·28	15·43	–	10·49
	50·15	7·38	13·74	–	10·03
Females	51·60	7·27	14·54	47·67	10·32
	54·26	7·01	13·22	46·07	10·31

MEASUREMENTS (in mm in order of body lengths). Males: Body breadth : 0·20; 0·22; 0·20. Oesophagus length : 1·63; 1·67; 1·36. Head diameter : 0·043; 0·054; 0·052. Length of cephalic setae : 0·016 + 0·014; 0·018 + 0·017; 0·018 + 0·014. Amphid width : 0·015; 0·014; ?. Tail length : 0·42; 0·68; 0·73. Cloacal diameter : 0·13; 0·13; 0·11. Spicule length : 0·175; 0·181; 0·168. Gubernaculum length : 0·095; 0·078; 0·081. Distance of pre-cloacal supplement from cloaca : 0·134; 0·112; 0·103.

Females: Body breadth : 0·20; 0·19. Oesophagus length : 1·42; 1·47. Distance of nerve-ring from anterior : 0·39; ?. Head diameter : 0·056; 0·054. Length of cephalic setae : 0·017 + 0·013; 0·017 + 0·014. Amphid width : 0·016; 0·015. Tail length : 0·71; 0·78. Anal diameter : 0·10; 0·11. Distance of vulva from anterior : 4·92; 4·75. Egg length × breadth : 0·42 × 0·16; –.

DESCRIPTION. The cuticle is marked with very fine transverse striations. The mouth is bounded by three rounded lips each bearing a pair of small conical labial papillae. Internally the cuticle of each lip is modified into a small transverse bar from which radiate a series of longitudinal striations, becoming progressively shorter towards the interlabial positions (Figs. 10b, c and d). These are similar to the semi-lunar striations (terminology of Inglis, 1964) found in many members of the Enoplidae. There are ten cephalic setae, the submedian pairs being only slightly subequal in length. The cephalic capsule is relatively narrow and its posterior border is roundly lobed between the cephalic setae. The amphids are pocket-like with oval openings. They are displaced slightly dorsally. There are two or three short post-amphidal setae and a few other short setae scattered posteriorly to about the level of the nerve-ring. The buccal cavity varies in appearance depending on the angle from which it is viewed. It is basically conical and contains a large solid dorsal tooth with a rounded tip. There are no subventral teeth visible. There is no sexual dimorphism shown in the head. The oesophagus is

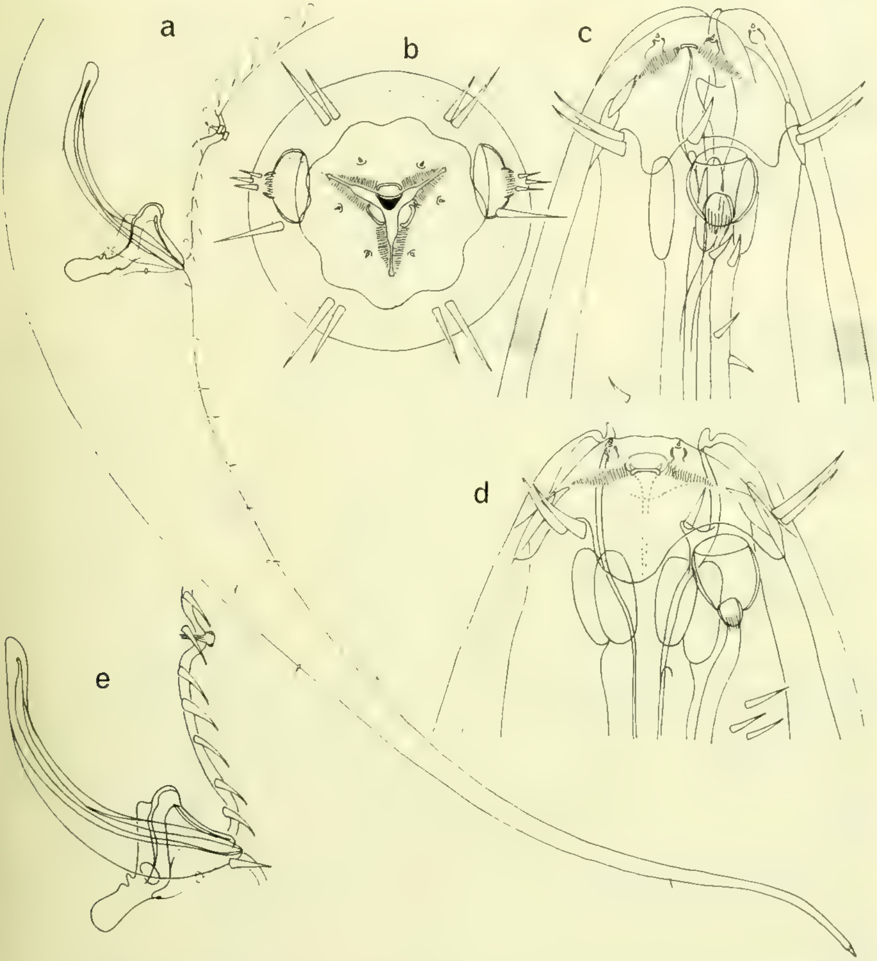

FIG. 10. *Synonchus alisonae* sp. nov. a, Male tail. b, *En-face* view of head. c and d, Heads of two males. e, Lateral view of spicules, gubernaculum and supplements.

cylindrical. The tail in both sexes is filiform with a pointed tip, but varies from 3·2 to 7·1 cloacal or anal diameters in length.

Male. The spicules are paired, equal and arcuate, with no marked proximal cephalization. The gubernaculum is of a complex structure. From the lateral view it has a triangular outline, and bears a solid rounded dorsal apophysis (Fig. 10e). There is a pair of ventral mamilliform supplements a short distance in front of the cloaca. Rows of subventral setae extend anteriorly from the cloaca about four times the supplement–cloaca distance, and posteriorly for some way down the length of the tail (Fig. 10a).

Female. The ovaries are paired, symmetrical and reflexed. The eggs are relatively elongate.

DISCUSSION. This species is characterized by the combination of a long filiform tail and relatively long cephalic setae. It appears to be closest to *S. filicaudatus* (Ditlevsen, 1926), another deep-water species. In Ditlevsen's species, however, the tail and cephalic setae are much shorter, and the gubernacular apophysis is triangular in shape.

Family **PHANODERMATIDAE**

Dayellus dayi Inglis, 1964

(Figs. 11a and b)

MATERIAL STUDIED. 13 ♂♂, 18 ♀♀ and 14 juveniles (2 ♂♂ and 2 ♀♀ measured below); B.M. (N.H.), Reg. Nos. 1972 : 436–481.

REPRESENTATION. Station 5047 : 7 ♂♂, 5 ♀♀ and 7 juveniles. Station 5060 : 6 ♂♂, 13 ♀♀ and 7 juveniles.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	58·04	8·22	27·53	–	5·92
	47·79	8·82	26·19	–	6·26
Females	62·30	10·92	31·74	51·96	8·41
	45·79	9·03	26·71	53·67	6·41

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·102 ; 0·131. Oesophagus length : 0·72 ; 0·71. Distance of nerve-ring from anterior : 0·275 ; 0·26. Distance of excretory pore from anterior : 0·058 ; 0·058. Head diameter : 0·012 ; 0·013. Length of cephalic setae : 0·014 + 0·0125 ; 0·016 + 0·0145. Tail length : 0·215 ; 0·239. Cloacal diameter : 0·071 ; 0·075. Spicule length : 0·130 ; 0·135. Gubernaculum length : 0·043 ; 0·045. Supplement length : 0·016 ; 0·018. Distance of supplement from cloaca : 0·036 ; 0·033.

Females : Body breadth : 0·135 ; 0·140. Oesophagus length : 0·77 ; 0·71. Distance of nerve-ring from anterior : 0·267 ; ?. Distance of excretory pore from anterior : ? ; 0·066. Head diameter : 0·013 ; 0·014. Length of cephalic setae : 0·014 + 0·0125 ; 0·015 + 0·013. Tail length : 0·265 ; 0·24. Anal diameter : 0·082 ; 0·060. Distance of vulva from anterior : 4·37 ; 3·44. Egg length × breadth : 0·165 × 0·090 ; –.

DESCRIPTION. The specimens conform exactly to the description provided by Inglis (1964), except that they are slightly smaller in many measurements, particularly the cephalic setae. The largest number of eggs found in any female is 18, 10 in the anterior uterus and 8 in the posterior uterus.

DISTRIBUTION. South Africa, South-east Arabia.

Crenopharynx fringilla sp. nov.

(Figs. 11c, d and e)

MATERIAL STUDIED. 9 ♂♂, 10 ♀♀ and 12 juveniles.

REPRESENTATION. Station 5047 : 7 ♂♂ and 2 ♀♀ (Syntypes) ; B.M. (N.H.), Reg. Nos. 1972 : 482–490 (only 3 ♂♂ and 2 ♀♀ measured below). Additional material : 7 ♀♀ and 12 juveniles ; B.M. (N.H.), Reg. Nos. 1972 : 491–509. Station 5060 : 2 ♂♂ and 1 ♀ ; B.M. (N.H.), Reg. Nos. 1972 : 510–512.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	32·34	4·76	15·51	–	5·66
	39·79	4·57	15·47	–	5·57
	40·00	4·63	14·74	–	5·60
Females	36·22	5·13	15·90	54·14	6·52
	34·63	4·63	15·48	56·23	6·58

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·175 ; 0·14 ; 0·14. Oesophagus length : 1·19 ; 1·22 ; 1·21. Distance of nerve-ring from anterior : 0·42 ; 0·44 ; 0·44. Head diameter : 0·019 ; 0·019 ; 0·019. Length of cephalic setae : 0·018 + 0·014 ; 0·015 + 0·012 ; ?. Tail length : 0·365 ; 0·36 ; 0·38. Cloacal diameter : 0·068 ; 0·064 ; 0·073. Spicule length : 0·345 ; 0·36 ; 0·37. Gubernaculum length : 0·081 ; 0·078 ; 0·095.

Females : Body breadth : 0·18 ; 0·19. Oesophagus length : 1·27 ; 1·42. Distance of nerve-ring from anterior : 0·43 ; 0·48. Head diameter : 0·019 ; 0·021. Length of cephalic setae : ? ; 0·017 + 0·014. Tail length : 0·41 ; 0·425. Anal diameter : 0·073 ; 0·075. Distance of vulva from anterior : 3·53 ; 3·70.

DESCRIPTION. The cuticle is smooth. The neck region is strongly tapered so that the head is relatively small. The head structure is exactly as described for other members of the genus by Inglis (1964). The cephalic capsule is lightly built with a lobed posterior margin, and the anterior end of the oesophagus projects anteriorly as three lobes (Fig. 11e). The cuticle supporting the six labial papillae which surround the mouth is sclerotized into crescentic areas. The ten cephalic setae are situated at the posterior edge of the cephalic capsule, six being slightly longer than the remaining four. A few scattered setae are present on the anterior end of the body, extending back about one-third of the oesophagus length. Setae are scarce on the middle of the body, but become more numerous again on the tail. The oesophagus is strongly tapered in association with the attenuation of the neck region, and becomes cellular posterior to the nerve-ring. The tail is elongate, with its distal end flagellate (Fig. 11c).

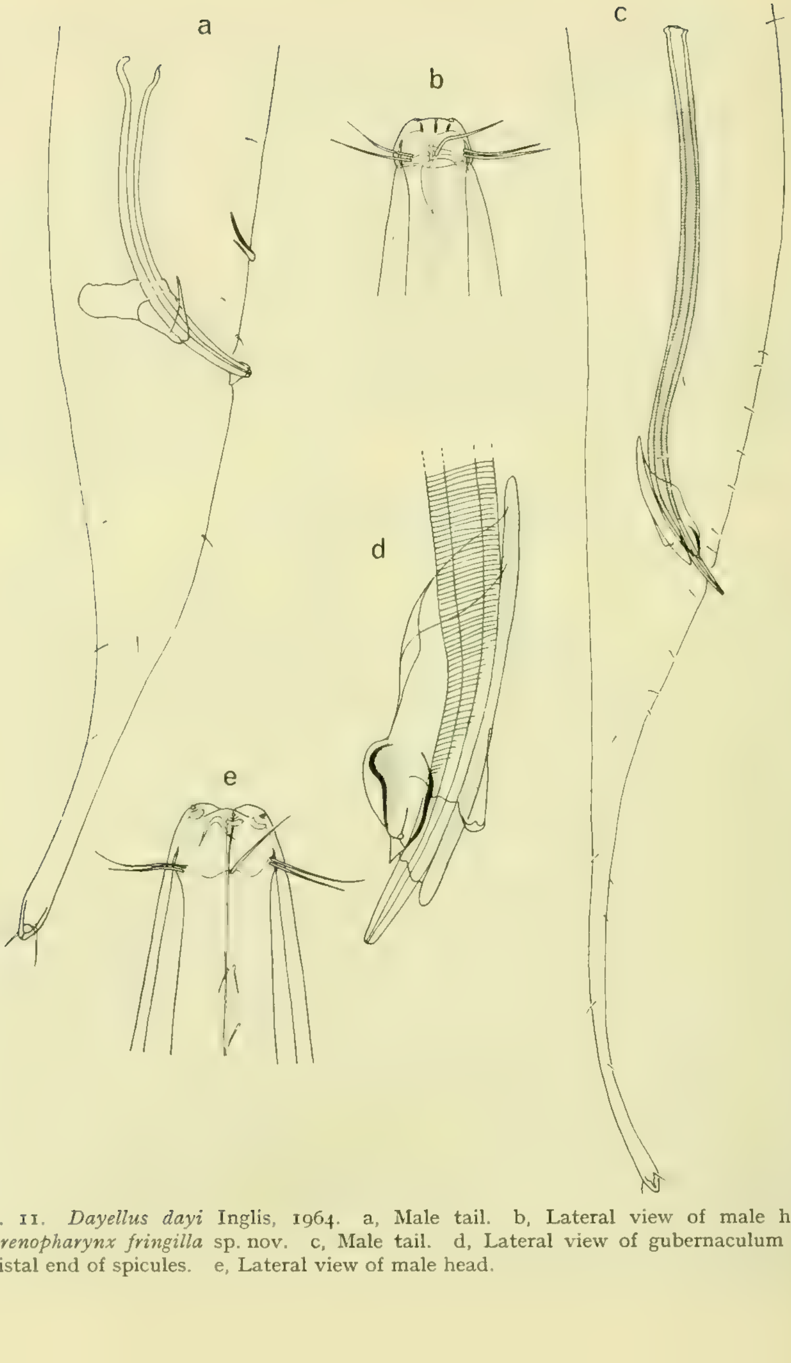

FIG. 11. *Dayellus dayi* Inglis, 1964. a, Male tail. b, Lateral view of male head. *Crenopharynx fringilla* sp. nov. c, Male tail. d, Lateral view of gubernaculum and distal end of spicules. e, Lateral view of male head.

Male. The spicules are elongate, paired and equal. They are slightly cephalate proximally and pointed distally. They are transversely striated for most of their length, except for short clear zones at the distal and proximal ends. Their ventral edges are not modified by any barbs or swellings. The gubernaculum has a complex folded structure and bears a pair of extensive lateral pieces terminating in sharp points (Fig. 11d). There is no pre-cloacal supplement.

Female. The ovaries are paired, equal, opposed and reflexed. One of the females not measured above contains three eggs in each uterus, a typical example measuring 0·216 × 0·097 mm.

DISCUSSION. This species is characterized by the combination of a long flagellate tail, spicules with no barbs or other modifications, and a gubernaculum with pointed lateral pieces. *C. crassus* (Ditlevsen, 1930) and *C. afra* Inglis, 1964, appear to be most nearly related to *C. fringilla*, but neither has the above combination of characters.

Family **ENOPLIDAE**

Mesacanthion southerni sp. nov.

(Figs. 12 and 13a and c)

MATERIAL STUDIED. 1 ♂ and 3 ♀♀ from Station 5034; 2 ♂♂ from Station 5047 (Syntypes); B.M. (N.H.), Reg. Nos. 1972 : 513–518. Additional material: 3 ♂♂ and 2 juveniles from Station 5047; B.M. (N.H.), Reg. Nos. 1972 : 519–523. Setae of specimens from Station 5047 are generally damaged.

REPRESENTATION. Station 5034 : 1 ♂ and 3 ♀♀. Station 5047 : 5 ♂♂ and 2 juveniles.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	33·91	5·57	14·44	–	3·90
	32·10	5·81	14·65	–	3·37
	32·80	?	14·91	–	3·28
Females	25·88	5·37	12·57	50·91	4·40
	29·82	5·51	13·70	51·28	5·07

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·115 ; 0·105 ; 0·100. Oesophagus length : 0·70 ; 0·58 ; ?. Distance of nerve-ring from anterior : 0·23 ; ? ; ?. Head diameter : 0·033 ; 0·035 ; 0·035. Length of labial setae : 0·012 ; ? ; ?. Length of lateral cephalic setae : 0·057 ; ? ; ?. Length of submedian cephalic setae : 0·048 + 0·039 ; ? ; ?. Tail length : 0·27 ; 0·23 ; 0·22. Cloacal diameter : 0·060 ; 0·055 ; 0·053. Length of right spicule : 0·32 ; 0·29 ; 0·30. Length of left spicule : 0·080 ; 0·067 ; 0·078. Length of gubernacular apophysis : 0·051 ; 0·045 ; 0·040. Length of supplement : 0·040 ; 0·034 ; 0·032. Distance of supplement anterior to cloaca : 0·100 ; 0·098 ; 0·082.

Females : Body breadth : 0·17 ; 0·17. Oesophagus length : 0·82 ; 0·92. Distance of nerve-ring from anterior : 0·26 ; 0·27. Head diameter : 0·039 ; 0·041. Length of labial setae : 0·013 ; 0·012. Length of lateral cephalic setae : 0·48 ; ?.

Length of submedian cephalic setae : 0·046 + 0·038 ; 0·038 + 0·033. Tail length : 0·35 ; 0·37. Anal diameter : 0·062 ; 0·068. Distance of vulva from anterior : 2·24 ; 2·60. Egg length × breadth : – ; 0·20 × 0·11.

DESCRIPTION. The cuticle is marked internally with faint transverse striations. The neck region tapers considerably from the base of the oesophagus : it is highly setose in the male (Fig. 13c), but only a few short scattered setae are present in the female. The head is typical of the genus. The three lips are relatively low. The lateral cephalic setae are slightly longer than the longer setae of each submedian pair. The cephalic capsule is punctate and deeply incised, with the cephalic setae situated at its anterior end (Fig. 12a). The mandibles have the usual appearance of two lateral rods united by an anterior curved bar. The three onchia are relatively large, and are equal in size. The oesophagus broadens considerably towards its base, but there is no posterior bulb. The tail is more or less evenly tapered throughout its length in both sexes (Fig. 13a).

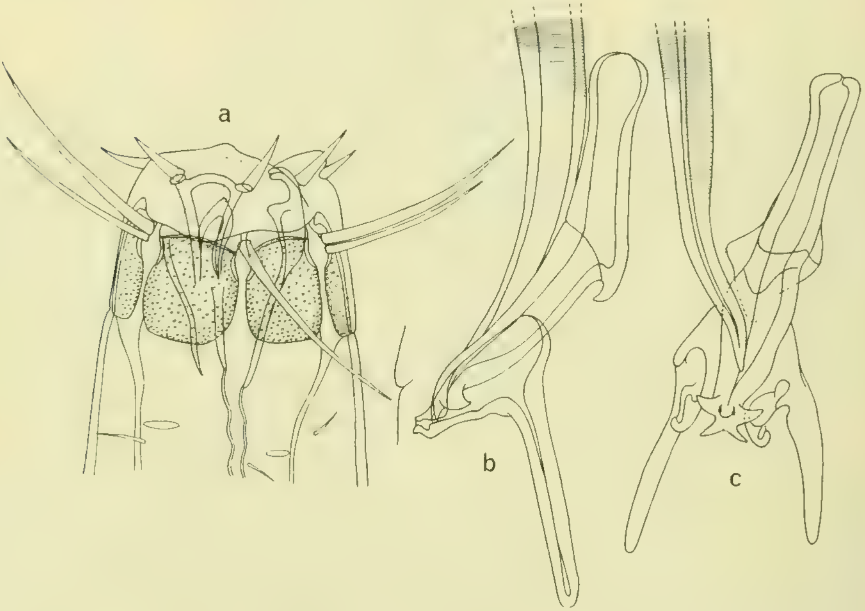

FIG. 12. *Mesacanthion southerni* sp. nov. a, Lateral view of female head. b, Lateral view of gubernaculum, left spicule and distal end of right spicule. c, Ventral view of gubernaculum, left spicule and distal end of right spicule.

Male. The spicules are asymmetrical. The right is elongate and transversely striated for most of its length, except near the distal and proximal ends (Fig. 13a). The left is short and smooth and is built in two halves with a fine suture between them. The proximal half bears a strong dorsal hook at its distal end, and the distal half terminates in four outwardly curving teeth (Figs. 12b and c). The gubernaculum is in two halves, each with an elongate posterior apophysis. The supplement is a simple cuticularized tube situated about half the right spicule length in front of the cloaca.

Female. The ovaries are paired, symmetrical, opposed and reflexed. The gravid specimen contains only one egg per uterus.

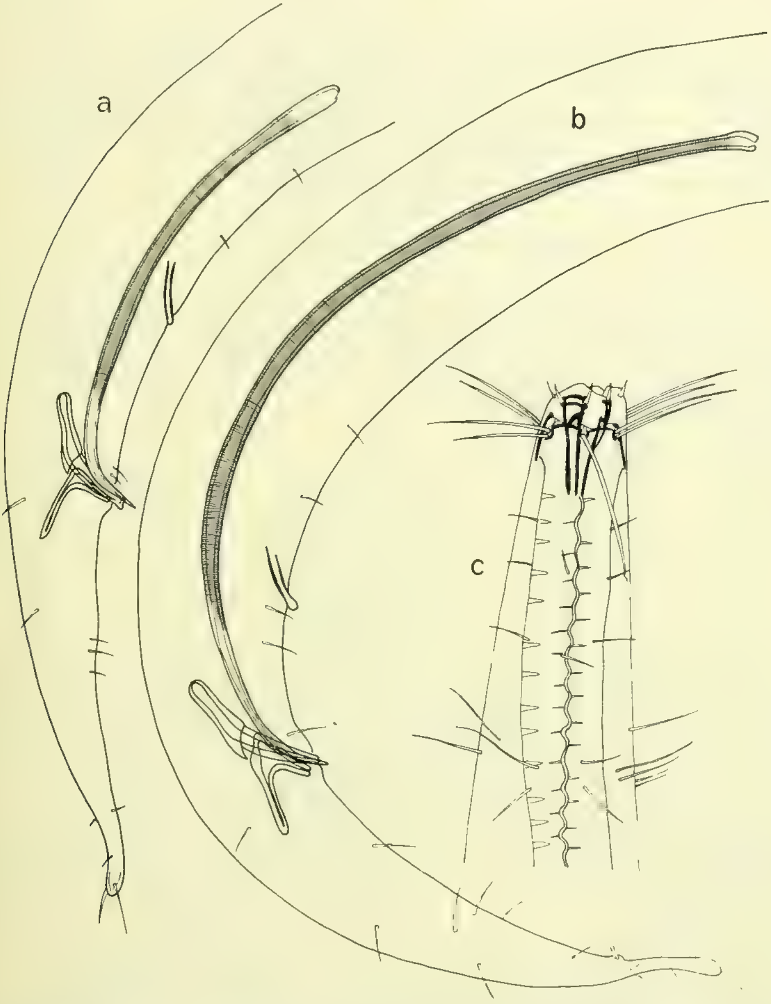

FIG. 13. *Mesacanthion southerni* sp. nov. a, Male tail. c, Anterior end of male. *Mesacanthion diplechma* (Southern, 1914). b, Male tail (drawn to same scale as a).

DISCUSSION. Because of the close similarity of the male reproductive complex, these specimens were at first assigned to *M. diplechma* (Southern, 1914). The spicular apparatus of this species has been redescribed by Ditlevsen (1934). However, close comparison with specimens of *M. diplechma* from the North Sea off Northumberland (Station A of Warwick and Buchanan, 1970) have revealed several differences which warrant specific rank. The male tail of *M. diplechma*, drawn from a North Sea specimen (B.M. (N.H.), Reg. No. 1972 : 538) is illustrated for comparative purposes in Fig. 13b. It will be noted that the right spicule of *M. diplechma* is much more elongate (0·54 mm in the illustrated specimen), so that the distance between the supplement and cloaca is less than a quarter of the right spicule length. *M. diplechma* bears a ventral setose papilla near the tail tip, which is absent in *M. southerni*. Another point of distinction is that the distal tip of the short spicule of *M. diplechma* bears three teeth (a point on which Southern and Ditlevsen agree), whereas *M. southerni* has four.

Mesacanthion arabium sp. nov.

(Fig. 14)

MATERIAL STUDIED. 3 ♂♂ and 3 ♀♀ (Syntypes) ; B.M. (N.H.), Reg. Nos. 1972 : 524–529. Additional material : 1 ♂ and 7 ♀♀ ; B.M. (N.H.), Reg. Nos. 1972 : 530–537.

REPRESENTATION. Station 5034.

DE MAN'S RATIOS.

	a	b	c	V %	Body length (mm)
Males	31·25	4·81	18·38	–	6·25
	37·00	4·93	16·91	–	5·92
	30·42	5·21	16·06	–	5·78
Females	33·42	5·16	16·71	53·07	6·35
	38·76	4·81	17·34	52·05	6·59
	32·85	4·94	16·85	51·45	6·57

MEASUREMENTS (in mm in order of body lengths). Males : Body breadth : 0·20 ; 0·16 ; 0·19. Oesophagus length : 1·30 ; 1·20 ; 1·11. Distance of nerve-ring from anterior : 0·32 ; 0·32 ; 0·28. Head diameter : 0·080 ; 0·080 ; 0·082. Length of labial setae : 0·025 ; 0·023 ; 0·024. Length of cephalic setae : 0·056 + 0·032 ; 0·065 + 0·030 ; 0·058 + 0·027. Length of cervical setae : 0·034 ; 0·029 ; 0·032. Tail length : 0·34 ; 0·35 ; 0·36. Cloacal diameter : 0·092 ; 0·090 ; 0·092. Spicule length : 0·60 ; 0·61 ; 0·57. Gubernaculum length : 0·126 ; 0·127 ; 0·120. Supplement length : 0·062 ; 0·059 ; 0·058. Distance of supplement anterior to cloaca : 0·23 ; 0·225 ; 0·22.

Females : Body breadth : 0·19 ; 0·17 ; 0·20. Oesophagus length : 1·23 ; 1·37 ; 1·33. Head diameter : 0·085 ; 0·085 ; 0·086. Length of labial setae : 0·024 ; 0·024 ; 0·024. Length of cephalic setae : 0·052 + 0·023 ; 0·055 + 0·027 ; 0·055 + 0·026. Tail length : 0·38 ; 0·38 ; 0·39. Anal diameter : 0·083 ; 0·080 ; 0·081. Distance of vulva from anterior : 3·37 ; 3·43 ; 3·38.

Description. The cuticle is smooth. The head is dome-shaped and the three lips relatively low. The four shorter cephalic setae are only about half the length of the remaining six. The cephalic capsule is deeply incised, with the cephalic setae situated at its anterior end (Fig. 14b). The posterior lobes of the capsule are lightly punctated. The mandibles are similar to those of the previous species, but much more heavily built. Their outer surface is sculptured with a series of

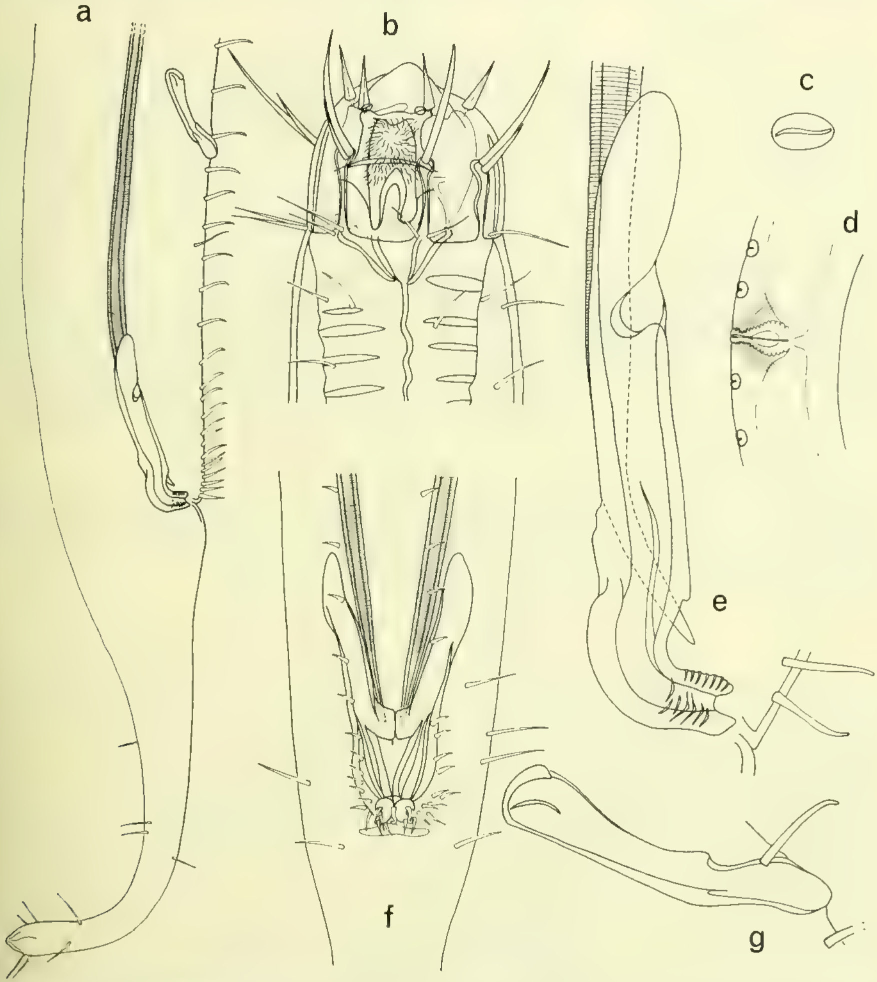

Fig. 14. *Mesacanthion arabium* sp. nov. a, Male tail. b, Lateral view of male head. c, Ventral view of vulvar organ of female. d, Lateral view of female vulvar region. e, Lateral view of gubernaculum and distal tip of spicules. f, Ventral view of male cloacal region. g, Lateral view of male pre-cloacal supplement.

short radiating lines. The onchia are equal in size, relatively smaller than in the previous species. The male bears a pair of cervical setae at the base of each incision of the capsule (i.e. 12 setae in all), and setae approximately the same length as the cervicals extend backwards from the head in six files approximately to the level of the nerve-ring. The paired cervicals and other setae are absent in the female. The oesophagus is cylindrical. The posterior half of the tail is cylindrical (Fig. 14a). In one female the three caudal glands extend 0·53, 0·63 and 0·77 mm in front of the anus.

Male. The spicules are elongate, and transversely striated along most of their length. The proximal tips (not illustrated) are non-cephalate. The gubernaculum consists of a pair of L-shaped pieces united in the middle by ventral strips (Figs. 14e and f). The distal ends bear a series of raised ridges. The supplement is a cuticularized tube of rather more complex structure than in most other members of the genus (Fig. 14g). Two subventral files of stout setae are present between the cloaca and the proximal tips of the spicules. They become more numerous near the cloaca.

Female. The ovaries are paired, symmetrical, opposed and reflexed. No specimens contain fertilized eggs. Transversely oval apparently glandular structures are present ventrally anterior and posterior to the vulva in eight of the ten available specimens. These are very prominent and open by long transverse slits (Figs. 14c and d). They probably aid adhesion to the male during copulation. They may be up to five in number, the distribution in the ten specimens being as follows :

anterior to vulva : 3 2 2 2 1 1 1 1 0 0
posterior to vulva : 2 2 2 1 2 1 1 1 0 0

Discussion. This species is characterized by the elongate spicules, the structure of the gubernaculum, the arrangement of cervical and cloacal setae and the organs associated with the vulva. In this latter feature it is unique.

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BIOLOGY AND FINE STRUCTURE OF *EUGLYPHA ROTUNDA* (TESTACEA: PROTOZOA)

By R. H. HEDLEY & C. G. OGDEN

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SYNOPSIS

Euglypha rotunda a fresh-water, moss and soil-inhabiting testacean has been established in clonal culture with a doubling time of between 33 and 45 hours; it is capable of reproducing in monoxenic culture with the bacterium *Klebsiella aerogenes* (strain NCIB 8017).

Full descriptions are given of the non-crystalline siliceous shell, the vegetative stage and the process of reproduction by simple division.

A detailed account of cytoplasmic fine structure reveals certain features of special interest: subpellicular microtubules; two or three contractile vacuoles each with a surrounding spongiome; a single well-developed Golgi apparatus with associated smooth and coated vesicles, and reserve siliceous plates stacked nearby; a well-defined region of endoplasmic reticulum, with a high concentration of ribosomes, surrounding the nucleus; the presence of a polysaccharide cement or glue binding the siliceous plates of the shell; microfilaments in the pseudopodia; and the occurrence of cross-striated fibrils in the cyst membrane of encysted individuals.

The habit of individuals clumping together to form rosette groups with cytoplasmic connections between them is described; the alignment of masses of microfilaments in these regions to form stress areas or desmosome-like structures is noted.

INTRODUCTION

THE widely distributed, fresh-water, soil- and moss-inhabiting rhizopods belonging to the genus *Euglypha* have attracted little attention by cytologists and protozoologists since an early study of *E. alveolata* by Schewiakoff (1888). Most of the work on these organisms has been concerned with faunal surveys of testate amoebae; no study of the cytoplasmic ultrastructure has been reported previously.

The present account concerns the biology and fine structure of cultured specimens of *E. rotunda* Wailes, 1911, isolated from collections made in Battersea Park, London, England.

Previous work – biology

The first general study of the cytoplasm of *Euglypha* was made by Carter (1865) who compared the internal structures of several protozoa. He observed that in *Euglypha* the nucleus normally occupies a posterior position, that union between two individuals is common and that there appear to be two types of structure associated with the division – 'ovules' (globular, nucleated 'cells') between four and fifty in number, and 'spermatozoids' (granules) both of which are situated close to the nucleus. Several authors (Gruber, 1881; Blochmann, 1887; Schewiakoff, 1888; Penard, 1890; Popoff, 1912, and Wailes, 1915) have described some aspects of nuclear division or reproduction in *E. alveolata*. Schewiakoff (1888) described and illustrated reproduction and nuclear division in *E. alveolata*. Penard (1890) reported that at conjugation the apertural teeth of two individuals locked together, and suggested that the increase in cytoplasmic volume at division was the result of water uptake. Blochmann (1887) observed copulation resulting in the formation of one extra large daughter cell. The types of reproduction were summarized by Wailes (1915) who suggested that there are three alternative methods: (i) spores which become amoeboid individuals, (ii) budding and (iii) simple division into two animals.

Penard (1890) reported that the pseudopodia of *Euglypha* appear to be stronger than those of naked amoebae and are apparently characteristic for each species. He also considered that the small granules in the body are not excretion granules as previously suggested by Bütschli (1880). The perinuclear cytoplasm was observed to be darkened with Giemsa stain by Popoff (1912). A detailed study of the cytoplasmic inclusions of *E. alveolata* by Hall & Loefer (1930) showed that the number of refractile bodies in the granular zone is approximately inversely proportional to the number of reserve shell-plates; the authors concluded from this that these refractile bodies might be the origin of the reserve plates.

Penard (1890) reported that at encystment the cytoplasm is contained behind a membrane within the shell and suggested that this is probably resorbed during excystment. He also described the unusual encystment of a large individual, in which numerous small, nucleated cysts could be seen. The same author (1902; 1940) described the encystment of *E. brachiata* (*armata*); in this species the cyst develops inside a smaller secondary shell which is formed within the parent shell. From a comparison of encystment in several testaceans, Thomas (1962) suggested that the large encysted test formed after copulation enabled the dissemination of the biotypes. In the most recent review of the biology of soil protozoa, Stout & Heal (1967) comment on the ecology and nutrition of some testaceans, including *Euglypha*.

In conclusion it appears that apart from a lot of information on the distribution of *Euglypha* we have a very limited understanding of any aspect of its biology.

Previous work – taxonomy

Several species of *Euglypha* were described by Penard (1890 ; 1902) before the first description of *E. rotunda* by Wailes (in Wailes & Penard, 1911). This species was considered to be distinct from *E. laevis* by the denticulate apertural-plates, the circular aperture and oval shape of the shell ; from *E. strigosa* by its size, unthickened apertural-plates and absence of spines ; from *E. ciliata* by its size and oval aperture and from *E. alveolata* var. *minor* by its shell-plates and oval shape as seen in section through the minor axis. It was recorded again by Wailes (1912) from the Shetland and Orkney Islands, who later (Wailes, 1915) redescribed the apertural-plates. In a review of the *British Freshwater Rhizopoda* fauna, Cash *et al.* (1915) described fourteen species of *Euglypha*, including *E. rotunda*, and recorded some additional localities. Some sizes of *E. rotunda* from soil in Italy were given by Grandori & Grandori (1934). The variation in shapes of apertural-plates was described by Decloitre (1950), who described the shell-plates and gave further data on size. In a later review of the genus, Decloitre (1962) lists descriptions for numerous specimens including *E. rotunda*. Recently, Decloitre (1964) reported upon the variation in size between specimens from Ceylon and Tasmania.

Two recent reports (Cambar *et al.*, 1964 and Mercier *et al.*, 1964) have described the surface ultrastructure of the shell of *E. strigosa* and a *Euglypha* sp., from metal and carbon-shadowed preparations.

The classification of the family Euglyphidae adopted here is that proposed by Loeblich & Tappan (1961) :

Class	*RHIZOPODEA*	Von Siebold, 1845
Subclass	*FILOSIA*	Leidy, 1879
Order	GROMIDA	Claparède & Lachmann, 1859
Superfamily	**EUGLYPHACEA**	Loeblich & Tappan, 1961
Family	**EUGLYPHIDAE**	Wallich, 1864 ;
	test hyaline, symmetrical, elongate, composed of rounded siliceous scales, aperture rounded or elongate ; one nucleus.	

MATERIAL AND METHODS

Euglypha rotunda was isolated from samples of sphagnum moss, weed and mud collected from ponds in Battersea Park, London, in November, 1967. Initially, rough cultures were obtained by allowing small portions of these samples to stand in a shallow layer of the culture liquid at room temperature, 18–20°C. Agnotobiotic cultures were kept in small plastic containers on a thin layer of agar agar (1 per cent in distilled water), and covered by a shallow layer of culture liquid. A sterilized wheat grain was added to the agar just before it set. The basal culture liquid was a 5 per cent (w/v) solution of soil extract in distilled water, to which nutrient salts were added so that the final culture medium contained 100 mg/l^{-1} sodium nitrate and 15 mg/l^{-1} sodium dihydrogen orthophosphate.

Single active animals were isolated to produce clonal cultures. Of twenty such cultures started only four reproduced, three within four days and the other after fourteen days. One clone was used subsequently to produce the working cultures and this clone is now registered (No. 1520/1) and maintained at the Culture Centre of Algae and Protozoa, The Natural Environment Research Council, Cambridge, England. The animals which feed and reproduce readily were sub-cultured approximately every four or five weeks.

Cultures made available to Dr H. Netzel (Zoologischen Institut der Universität Tübingen) have been used to produce cine-photomicrographs of locomotion and reproduction (Netzel, 1971).

Optical microscopy

The animals were examined either live, or after fixation, by both phase-contrast and bright-field microscopy. Smears fixed in Schaudinn's fluid were stained with borax carmine and iron haemotoxylin. Clumps of animals for sectioning were fixed in Schaudinn's and embedded in agar (Harris, 1965), the sections being stained with either Mayer's haemalum, toluidine blue or Mallory's triple stain.

Scanning electron microscopy

Specimens removed from the cultures were either cleaned by transferring them directly from the culture vessels through several changes of triple-distilled water or, alternatively, first fixed in osmium textroxide or glutaraldehyde and then washed. They were subsequently pipetted with a minimum of water onto a cover-slip, which had been cleaned in acetone and polished with lint-free tissue, to which they adhere quite well on drying. Single specimens for use in the examination of individual siliceous shell-plates were cleaned by immersion in a slightly acidic solution of hydrogen peroxide (20 vol.) for approximately thirty minutes, prior to washing. Suitably clean animals were then placed individually onto small pieces of cleaned cover-slip. To this a drop of concentrated sulphuric acid was added, and evaporated by gentle heating. This liberates the plates from the organic cement material. The prepared cover-slips were then glued to a ' Stereoscan ' specimen stub with ' Silver Dag ', an electrically conductive paint, and coated evenly with 10–15 nm of gold in a coating-unit using the apparatus described by Harris *et al.* (1972). Specimens were examined in a Cambridge Stereoscan Mk II at either 15 or 20 kV, and the results recorded on Ilford HP3 35 mm film.

Transmission electron microscopy

The animals were fixed at room temperature for 15 minutes in 1 per cent glutaraldehyde in 0·05 M Sorensen's phosphate buffer with 0·015 M calcium chloride, followed by 10 minutes in 3 per cent glutaraldehyde in the same buffer, and finally post-fixed in 1 per cent osmium tetroxide in 0·1 M Sorensen's phosphate buffer. After rapid dehydration in ethanol the specimens were embedded in Epon 812.

Sections were cut with a Du Pont diamond knife on either a Porter–Blum or Reichert ultramicrotome, and stained with a saturated solution of alcoholic uranyl acetate and Reynold's lead citrate. Some animals for whole-mount examination were placed on Formvar-coated, gold grids in a drop of fresh water. When they had extended their pseudopodia, a Petri dish containing a few drops of 2 per cent osmium textroxide was inverted over the grid for 1–2 minutes. Osmium vapour fixes the animals and pseudopodia instantly. The excess liquid was removed and the grid allowed to dry. Sections mounted on gold grids were used for the detection of periodic acid-reactive carbohydrates, according to the silver methenamine technique of Rambourg (1967). The micrographs were obtained using an A.E.I. EM6B electron microscope operating at 60 kV and recorded on Ilford's 'special lantern contrasty' plates.

DISTRIBUTION

E. rotunda is commonly found in damp and wet mosses, soil, forest litter and standing water. A full list of locality records and references was recorded by Bonnet & Thomas (1960) and Decloitre (1962; 1964).

The following list illustrates the geographically widespread distribution:

EUROPE:	Spitzbergen, England, Scotland, Ireland, France, Belgium, Germany, Hungary and Italy.
NORTH AMERICA:	Greenland, Canada and the United States of America.
SOUTH AMERICA:	Argentina, Colombia, Peru and Venezuela.
AFRICA:	Angola, Morocco and Madagascar.
ASIA:	Ceylon, Java, Sumatra and Tahiti.
AUSTRALASIA:	New Zealand and Tasmania.
ANTARCTICA:	South Georgia.

MORPHOLOGY AND VARIATION

The shell is small, varying in length from 34 to 56 μm and having a breadth of 14 to 24 μm (Pl. 1, fig. A); it is elliptical in shape through both the minor and major axes. The aperture is terminal and circular, having a diameter of 6 to 10 μm and is surrounded by between eight to fourteen, evenly spaced, apertural-plates (Pl. 1, fig. D; Pl. 2, fig. B), although the most frequent number of plates is eight, nine or ten. Each apertural-plate is circular in shape, between 4·5 and 5·5 μm long, 3·6 and 4·5 μm wide, 0·59 and 0·82 μm thick (at its widest point) and carries a large median tooth, with either two or three smaller teeth situated on each side (Pl. 1, figs. C & D). The shell-plates range from 5·0 to 7·3 μm in length, 2·9 to 4·5 μm in width and 0·16 to 0·27 μm thick (Pl. 1, fig. B), and are arranged regularly in alternate longitudinal rows (Pl. 1, fig. A). Shell-plates overlap to a certain extent at the lateral margins and in the posterior region (Pl. 2, fig. C). At the posterior extremity (Pl. 2, fig. D) the shell appears to end abruptly.

An electron probe microanalysis of some shells showed that they had a high silica content and an almost negligible amount of calcium. No evidence of crystalline material was obtained from electron diffraction examination carried out on both sectioned material, and on shells cleaned of most tissue by sodium hypochlorite, separated ultrasonically and washed with distilled water. It is concluded that the shell-plates are composed of a high percentage of amorphous silica.

Variation in structure of the shell appears to be confined to the occasional formation of an extra large individual with more than the normal number of shell-plates. Such forms appear to result from conjugation of a pair of, or possibly more, mature specimens. The process is similar to that described by Blochmann (1887) and Penard (1902 ; 1940), in which it appears that the cytoplasm and plates for two daughter-cells are united to form a single shell. This possibly accounts for the specimens that have extra, unevenly spaced apertural-plates. Nevertheless, these animals appear to have a normal arrangement of shell-plates.

REPRODUCTION

Observations by optical microscopy indicate that the formation of a daughter-cell by means of simple division commences with cytoplasmic movement of the parent to produce a short, thick, pseudopodial trunk. As the apertural-plates of the daughter-cell emerge they are arranged around the outside of the pseudopodial trunk and lie with their teeth opposed to those of the parent. This is followed by rapid movement of the shell-plates from parent to daughter, where they become arranged in a regular pattern. The shell-plates are always added in sequence so that the plates at the terminal region are positioned last. When the plates are in their final position the daughter-cell rocks from side to side. At about this time the first signs of cytoplasmic transfer are seen ; globular vacuoles pass from parent to daughter-cell, and the nucleoles of the nucleus change in density and shape. When the shells are of equal size the granular material of the parent moves to the apertural region and the nucleus becomes indistinct. As the nucleus begins division it is no longer visible due to the rapid movement of granular material between parent and daughter. The plasmalemma and the contractile vacuoles are now visible in the daughter-cell. The rate of cytoplasmic movement then decreases and a nucleus appears in the posterior region of each cell. At the same time a granular band, slightly anterior to each nucleus, becomes evident. There is now a period of apparent inactivity before pseudopodia are extended and independent movement begins. The total time taken for such division is approximately sixty minutes although the shell itself is produced more rapidly, in approximately fifteen minutes.

In order to estimate the length of time required to double the population (doubling time), three identical cultures were established and maintained under similar conditions. Daily counts of the number of animals observed were recorded, and these have been used to produce growth curves (Text-fig. 1) from which the doubling time has been calculated to be between 1·4 to 1·9 days.

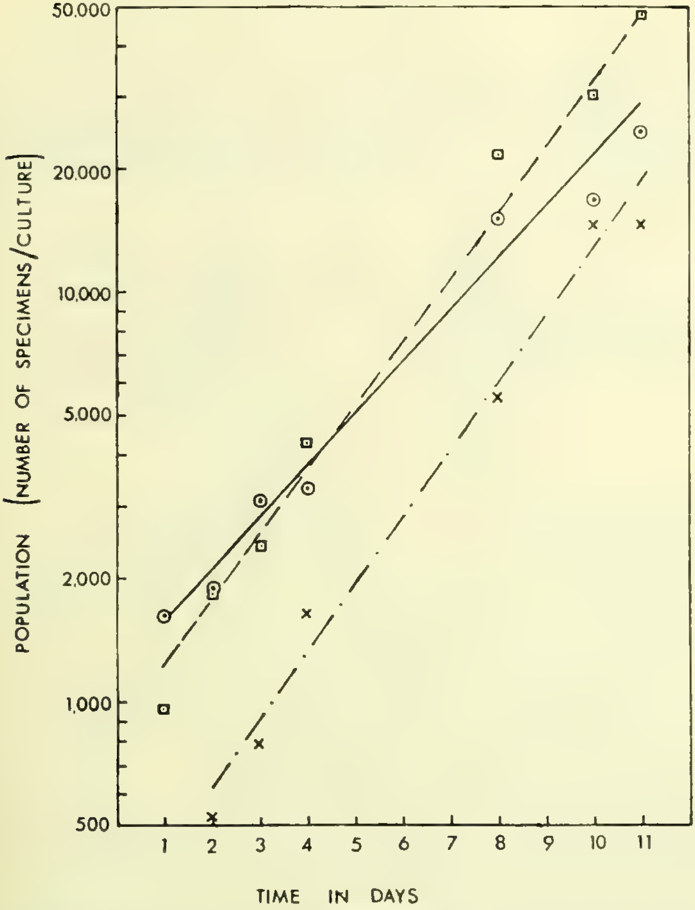

FIG. 1. Growth curves for *E. rotunda* in culture. The symbols represent three replicate cultures through which curves have been fitted by eye. The calculated doubling times are ⊡ – – ⊡ 1·9 days ; ⊙——⊙ × 1·4 days and —·— × 1·85 days.

FOOD

Although the cultures in the laboratory were normally grown on a mixed bacterial flora, it is noted that successful cultures can be maintained using a single bacterium as the sole food source. Agar plates, streaked with *Klebsiella aerogenes* (strain NCIB 8017) and covered with the *Euglypha* culture medium, were incubated overnight at 25°C to establish the bacteria. The plates were then inoculated with washed *Euglypha* and incubated in the dark at 20°C. Sub-cultures were made at weekly intervals and under these conditions the *Euglypha* appeared to grow and reproduce well.

CYTOLOGY

Vegetative stage

The cytoplasm normally occupies the whole of the shell cavity and is enclosed by a plasmalemma (Text-fig. 2, Pl. 3, fig. A). Pellicular microtubules lie beneath the plasmalemma (Pl. 6, fig. B) running in an antero-posterior direction. They are not uniformly spaced, but occur often in associated groups of three or four. Porter (1966) in a review of microtubules suggested, on the evidence then available, that they might function as cytoskeletal structures. However, the presence of sub-pellicular microtubules would appear to be unnecessary in *E. rotunda* as the shell delimits the shape of the cell. Ovoid or spherical mitochondria having tubular cristae and a dense granular matrix (Pl. 3, fig. D) are distributed throughout the cytoplasm. The nucleus is usually spherical, between 4·2 and 5·9 μm in diameter, and enclosed within two tripartite membranes (Pl. 3, fig. C). The nuclear matrix is finely granular with small concentrations of chromatin scattered throughout. A prominent and densely stained nucleolus, of variable shape, occupies the centre of the nucleus. Cisternae of granular endoplasmic reticulum arise from the outer membrane of the nuclear envelope and occupy a large compact region around the nucleus (Pl. 3, fig. D). Due to the concentration of ribosomes, this region is more heavily stained than the remainder of the cytoplasm. A region of large vacuoles, usually containing electron-dense material, lies immediately anterior to the endoplasmic reticulum. This electron-dense material appears to be leached out in some preparations and the vacuoles appear empty (Pl. 3, figs. A & D). This region corresponds to the ' pigment zone ' of optical microscope descriptions of some earlier authors (Text-fig. 2). Two or three contractile vacuoles are present at the same level as the large vacuoles, but lie in the endoplasmic reticulum (Pl. 3,

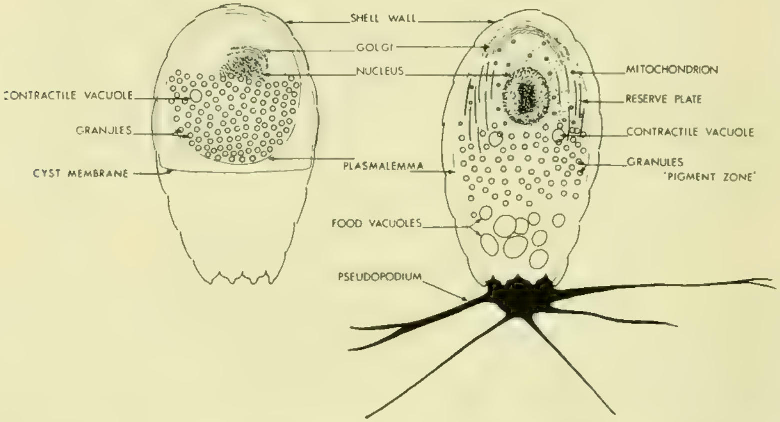

FIG. 2. Diagram of cyst and vegetative stage of *E. rotunda* showing the arrangement of the main organelles.

fig. A). They are usually surrounded by numerous vesicles which are continuous with the lumen of the vacuole. Ribosomes appear to be absent from that area surrounding the contractile vacuole which contains the canicular system or spongiome (Pl. 7, fig. A). The spongiome tubules have similar internal and external fibrillar coats to those found in *Acanthamoeba castellanii* (Bowers & Korn, 1968) and *Crithidia fasciculata* (Brooker, 1971). The contractile vacuoles discharge directly into the cavity of the shell.

There is a single well-developed Golgi apparatus situated adjacent to the base of the concentrated endoplasmic reticulum surrounding the nucleus (Pl. 3, figs. A & D). In section it is U-shaped, the base lying in a channel or groove of the endoplasmic reticulum close to the nucleus, whilst the arms extend upwards into the lateral margins. Both smooth and coated vesicles are seen to be associated with the margins of the Golgi saccules. The anterior third of the cytoplasm is occupied by numerous food vacuoles which have a single unit membrane and may contain both food organisms and waste material (Pl. 3, fig. D).

Siliceous plates and cement

There are two distinct types of siliceous plates: firstly, eight to fourteen apertural-plates which are thickened anteriorly at the base of the median tooth, tapered posteriorly and confined to the apertural region; and secondly, approximately one hundred and twenty shell-plates of uniform thickness which are arranged to form the rest of the shell. The plates overlap each other slightly and are held together with an organic cement or glue (Pl. 4, fig. E). They are composed mainly of amorphous silica which is electron-dense in sectioned material (Pl. 4, figs. A & B). Complete sections of individual plates may be obtained (Pl. 4, figs. E & F) although more frequently they fracture in an apparently uniform manner (Pl. 4, fig. D; Pl. 5, fig. H).

Prior to cell-division reserve-plates are formed in the region of the granular vacuoles and endoplasmic reticulum, but close to the Golgi apparatus. Each reserve-plate is enclosed in a membrane-bound vacuole (Pl. 4, fig. F) and is usually situated at the periphery of the cytoplasm (Pl. 4, fig. B). The area between the reserve-plates and the Golgi apparatus contains many vesicles of both the smooth and coated type (Pl. 4, fig. C). Vesicles of a similar nature have been reported to be associated with the Golgi apparatus and scale-containing vesicles in the Haptophyceae – *Prymnesium* and *Chrysochromulina* (Manton, 1966; 1967a, b), and the coccolithophorids – *Coccolithus pelagicus* and *Cricosphaera carterae* (Manton & Leedale, 1969). Although we have no evidence that these vesicles discharge into the reserve-plate vacuoles, their close proximity suggests some correlation. As more plates are formed they become packed in ranks around the nucleus (Pl. 4, fig. A). The reserve apertural-plates are usually found in the most posterior position with their dorsal teeth facing inwards (Pl. 4, fig. D).

Sections of specimens fixed with glutaraldehyde, but without the inclusion of heavy metals in this or subsequent procedures, were examined, in an attempt to locate sites of silica deposition. Apart from the siliceous plates, however, no other electron-dense regions were observed (Pl. 4, figs. A & B).

Previous reports on the formation of siliceous structures in other organisms have dealt mainly with either sponge spicules (Travis *et al.*, 1967 ; Drum, 1968 ; Garrone, 1969 ; Fjerdingstad, 1970) or the diatom frustule (Desikachary & Dweltz, 1961 ; Drum & Pankratz, 1964 ; Lauritis *et al.*, 1968). Such structures are formed in similar membrane-bound vesicles to those described here for *E. rotunda*. The close association of smaller vesicles in *E. rotunda* which could coalesce with the silicon deposition vesicles are also observed by Lauritis *et al.* (1968) in the diatom *Nitzschia alba*. Fine structure studies have shown that sponge spicules in *Spongilla lacustris* and *Haliclona rosea* are formed initially on an axial thread of protein (Fjerdingstad, 1970 ; Garrone, 1969) and an analysis by Desikachary & Dweltz (1961) shows that a small amount of organic material is also present in the diatom frustule. Fjerdingstad (1970) suggests that the silica in the sponge spicule of *Spongilla lacustris* is arranged in parallel ' silica units ' of regular structure. Although we have observed similar ' units ' in *E. rotunda*, we consider that this is only the result of imperfect sectioning of hard material.

Despite many observations on the formation of siliceous structures in plants and animals very little is known of the source of the silicon or of silicon metabolism. The biochemical and physiological problems involved in silicification in organisms are virtually unexplored.

A minimum of organic cement or glue is present to hold the plates in position and maintain the specific shape. The cement is a fine fibrillar material (Pl. 4, fig. E), similar to that found in those membrane-bound vesicles that lie close to the periphery of the cytoplasm (Pl. 5, fig. B), mainly in the anterior body-region (Pl. 5, fig. H). Such vesicles have been found fused with the plasmalemma and discharging their contents into the shell-cavity (Pl. 5, fig. A). The contents of these vesicles stain strongly for polysaccharide (Pl. 5, fig. C), using the silver methenamine technique (Rambourg, 1967), as do the organic cement connections between the plates.

Variation in the composition of these vesicles is sometimes seen, in which the contents have a regular striated structure and occasionally there is a strongly electron-dense area in the polar regions (Pl. 5, figs. D & E). The striations or bands are 12 nm apart and are separated by a fibrillar region 25 nm wide.

Pseudopodia

The filose pseudopodia of *E. rotunda* are usually straight, do not appear to anastomose and radiate from the apertural region (Text-fig. 3 ; Pl. 3, fig. B). Over most of their length the pseudopodia are of uniform thickness, tapering at the extremities. They have a maximum length of 50 μm and a maximum thickness of 2 μm. The animal moves horizontally on glass, by the extension of unattached pseudopodia, which adhere at the tip and then shorten to exert traction. In this way the animal normally moves at approximately 2 μm per second. The pseudopodia are extended quickly and apparently at random, but are also capable of rapid withdrawal. In addition to horizontal movement the animal often moves with the shell held in an upright position above the pseudopodia. In this condition it appears that the tips of the pseudopodia act as feet, being retracted only slightly before moving and reattachment. Viewed from above the shell progresses with an uneven rolling motion, rather than a smooth gliding action.

The fine structure of the pseudopodia appears to consist of ground-plasm, limited by a membrane, containing microfilaments. Microtubules are apparently absent, although sections through cytoplasmic extensions within the test do contain microtubules. This is consistent with the recent observations on *Difflugiella* sp. in which microtubules were numerous in pseudopodia within the mouth, but extended for only 1–2 μm into pseudopodia 20–30 μm long (Griffin, 1972).

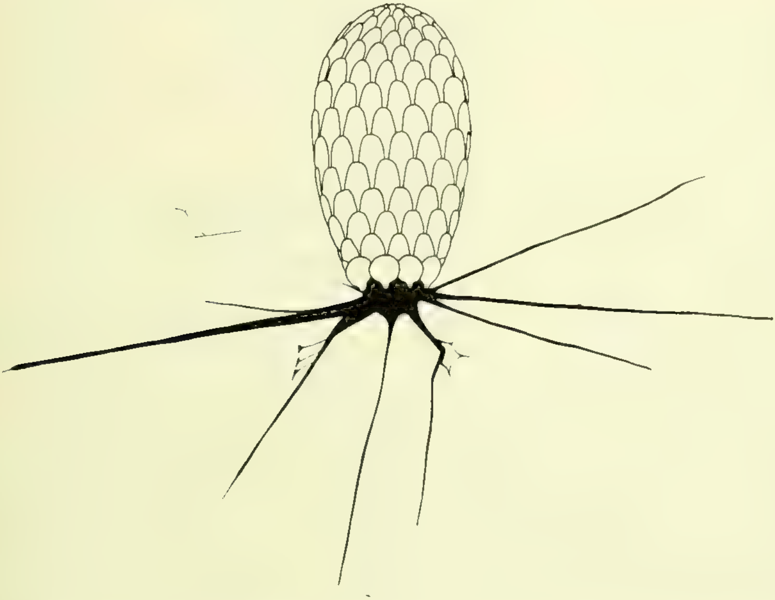

FIG. 3. Diagram of adult *E. rotunda* showing a typical arrangement of filose pseudopodia, drawn from life.

Reports of similar microfilaments have been described from slime moulds (McManus & Roth, 1965) and several amoebae, both naked (Daniels & Breyer, 1967; Pollard *et al.*, 1970; Pollard & Korn, 1971) and with shells (Wohlman & Allen, 1968; Moraczewski, 1970; Griffin, 1972). Microfilaments in the testate amoeba *Difflugia* have been demonstrated by Wohlman & Allen (1968) to be formed during pseudopod extension, and they suggest that these fibrils participate in forcible pseudopod retraction during cell locomotion. In the naked amoeba, *Amoeba proteus*, Pollard & Ito (1970) described thick and thin filaments, the latter being associated with an increase in viscosity, although both are required for movement. More recently they (Pollard & Korn, 1971) found that the thin filaments were indistinguishable from F-actins obtained from muscle (Huxley, 1963), *Acanthamoeba* (Pollard *et al.*, 1970) and the slime mould *Physarum* (Nachmias *et al.*, 1970) ; it was concluded that these structures are involved in motility. Using the drug cytochalasin B, Wessels *et al.* (1971) demonstrated that microfilaments are the contractile machinery of non-muscle cells, and suggested that the evidence for this behaviour is overwhelming.

Rosette groups

Some two or three weeks after clonal cultures are established numerous animals appear linked in rosette-like groups (Pl. 2, figs. A & E). Individuals forming these rosettes are joined by cytoplasmic connections containing mitochondria, numerous vesicles and microfilaments (Pl. 2, fig. F, Pl. 6, fig. A). The majority of these vesicles are small and do not appear to have any characteristic contents (Pl. 6, fig. A). The microfilaments are usually straight although they may be seen to curve when passing through the aperture (Pl. 7, fig. H) ; they are found both inside (Pl. 6, fig. C) and outside the shell (Pl. 7, fig. H). These structures appear to have a binding function, as they form adhesion plaques of concentrated microfilaments at those points to which they become attached or anchor (Pl. 5 fig. H, Pl. 6, fig. B). Using the terminology of Bennett (1969) this would be a ' desmosome '. We make no attempt to classify it further, however, as the types defined by Bennett (1969) refer to individual cell junctions. In the case of *E. rotunda* the junctions occur between cells sharing cytoplasm and are both internal and external to the shell.

The microfilaments in these intracellular connections may be capable of transmitting tensile forces through the adhesive plaques which will help to retain the rosette formation, and in this way may be similar to the forces present at desmosome junctions. Similar attachment areas are reported by Buckley & Porter (1967) from cultured rat embryo cells associated with ' stress fibers ' (= bundles of microfilaments). They suggested that these ' stress fibers ' are concerned in stabilizing areas of cellular attachment as well as resisting forces that stretch the cell.

Certain morphological changes have been detected in the cytoplasmic contents of those animals in rosette formation. In the mitochondria the intracristate space becomes enlarged and tubular material appears (Pl. 5, figs. F & G). Similar structures have been reported previously from encysting *Acanthamoeba* by Vickerman (1960, 1962), Bowers & Korn (1969) and more recently from encysting *Bodo caudatus* by Brooker & Ogden (1972). Bowers & Korn (1969) suggest that these features are probably related to starvation rather than encystment. The exocytoic vacuoles are seen at this time to contain reserve-plates in addition to the normal undigested materials (Pl. 6, fig. D).

One unusual feature of these rosette-like groups is that although the evidence suggests either starvation or encystment, bacteria are still seen to be engulfed (Pl. 6, fig. A).

Testate amoeba in which individuals clump together and between which the cytoplasm is connected have been reported previously ; *Arcella vulgaris* (Reynolds, 1939), *Difflugia elegans* (Erth, 1965) and *Difflugiella* sp. (Griffin, 1972). Clumping without cytoplasmic connections between individuals has also been reported in cultures of other protozoa. Band & Mohrlok (1969) found that the soil amoeba, *Mayorella palestinensis*, formed clumps alone and with another amoeba, *Hartmannella rhysodes*, although the latter species did not clump in pure culture.

Opinions differ over the factors which induce the formation of such groups in amoebae. Reynolds (1939) considers that this behaviour is related to nutritional factors, and observes that when such groups of *Arcella vulgaris* are transferred to fresh culture media or spring water they separate. Band & Mohrlok (1969) suggest that in *Mayorella palestinensis* it is temperature dependent and not associated with starvation and encystation. They found no extra- or intracellular changes on examination at the ultrastructural level, but showed that these cells became interlocked. Our observations would indicate that the cause is either starvation or encystation.

Cyst

Encysted animals occur in cultures usually four or five weeks after inoculation. The cyst is contained within a cyst-membrane which lies close to the shell wall, except in the anterior region where it forms a seal across the aperture of the shell. In mature cysts the membrane retracts so that it lies close to the mid-point region of the shell (Text-fig. 2, Pl. 7, fig. C).

The cyst-membrane consists of amorphous fibrillar material, similar to the organic cement material found joining the body-plates. In mature cysts it becomes striated (Pl. 7, fig. D) with striations being visible mainly at positions where the plates do not join or overlap, for example, at the posterior end of the shell (Pl. 7, fig. G). In addition, striations occur in the thickened region across the middle of the shell (Pl. 7, fig. E). An unusual feature of this portion of the cyst-membrane is that during the early stages of encystment, a layer of apparently unconnected membrane is enclosed in the fibrillar material (Pl. 7, fig. F) and is retained even in mature cysts.

The striated or banded appearance of the cyst-membrane (Pl. 7, fig. G) presumably reflects a fibrous protein composition. The fibrils are cross-striated, with a regular pattern being repeated every 40 nm (= axial period) and within each of these bands two alternating light and dark intraperiod bands of equal thickness are recognized. The limited detail from the available micrographs precludes further comment but it is noteworthy that cross-striated fibrils of the collagen type – not previously known to occur in protozoans – were reported recently in the rhizopod *Haliphysema* (Hedley & Wakefield, 1967).

During encystment the cytoplasmic volume is considerably reduced (Pl. 7, fig. C). There is a reduction in the number of mitochondria and they appear to be found only in the region of the endoplasmic reticulum. The matrix of the endoplasmic reticulum is reduced in size and appears dense compared with the remainder of the cytoplasmic matrix. The electron-dense vacuoles of the ' pigment zone ' are retained (Pl. 7, fig. C) but no reserve-plates are visible. As encystment proceeds the plasmalemma becomes progressively invaginated and the pellicular microtubules are no longer found close to it (Pl. 7, fig. B). Thin strands of cytoplasm connect the young cyst to the cyst-membrane (Pl. 7, fig. G), while in older cysts, these appear to be confined only to that portion of the cyst nearest to the unattached cyst-membrane. No apparent changes in the Golgi apparatus or the nucleus have been observed.

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NOTE

Since this paper was submitted for publication a brief account of the production of a new daughter-shell by *E. rotunda* is reported by Netzel (1972).

These observations were based on the present authors' original material.

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PLATE 1

A. Lateral view of *E. rotunda* showing the arrangement of shell-plates. × 2,300
B. Individual shell-plates. × 7,500
C. Lateral view of apertural-plates with two lateral teeth. × 7,500
D. Aperture of *E. rotunda* with fourteen apertural-plates ; note the thickened region associated with the median tooth and some plates (arrowed) with three lateral teeth. × 5,900

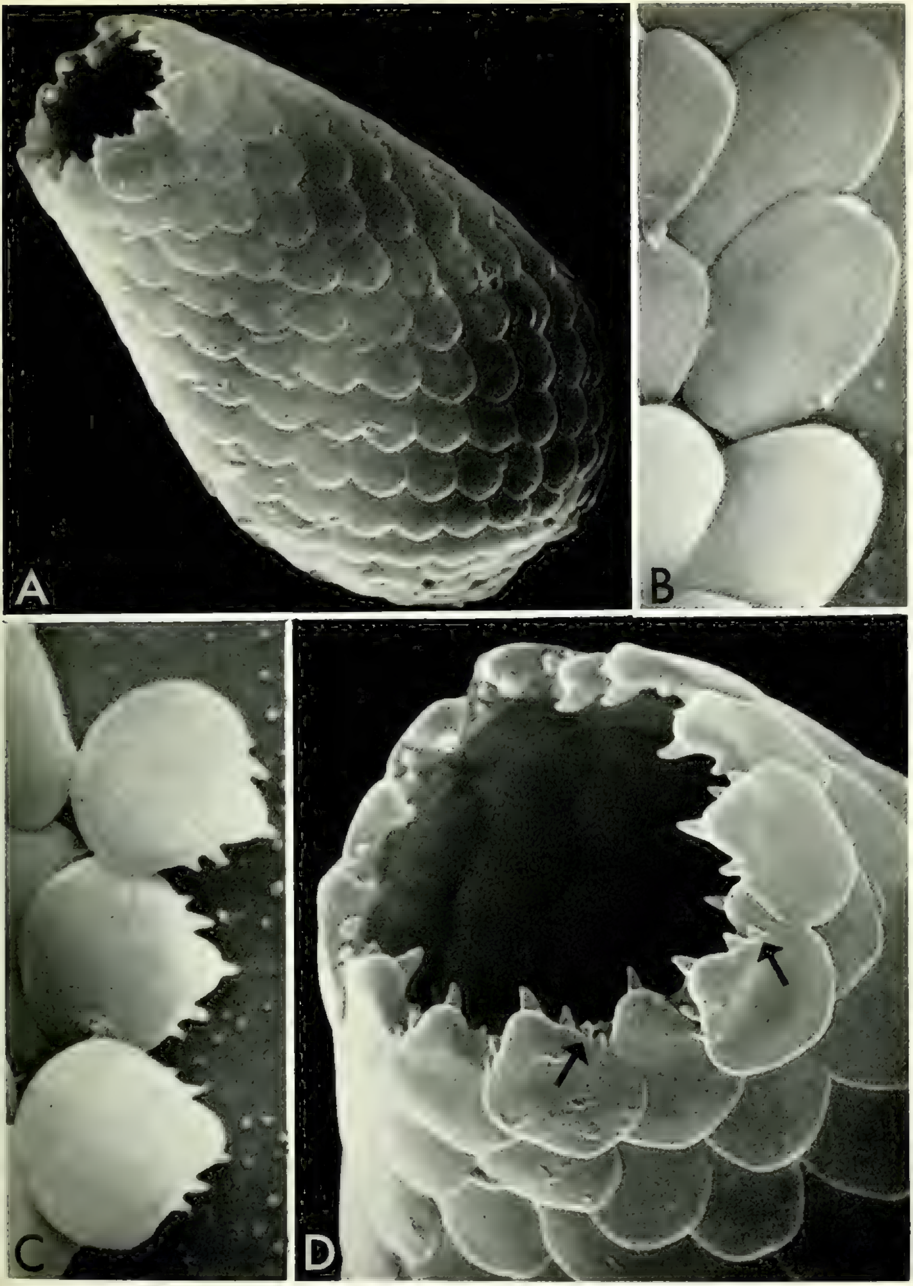
A
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PLATE 2

A Light micrograph of animals stained with eosin and Mayer's haemalum. × 250
B Specimen with ten, evenly spaced apertural-plates. × 6,650
C View of posterior region showing the arrangement of plates and lateral flattening of shell. × 2,850
D. Lateral view of posterior region showing the overlap of plates and blunt termination. × 4,280
E Group of six animals in ' rosette ' formation. × 675
F Cytoplasmic connections of ' rosette ' formation. × 5,000

PLATE 2

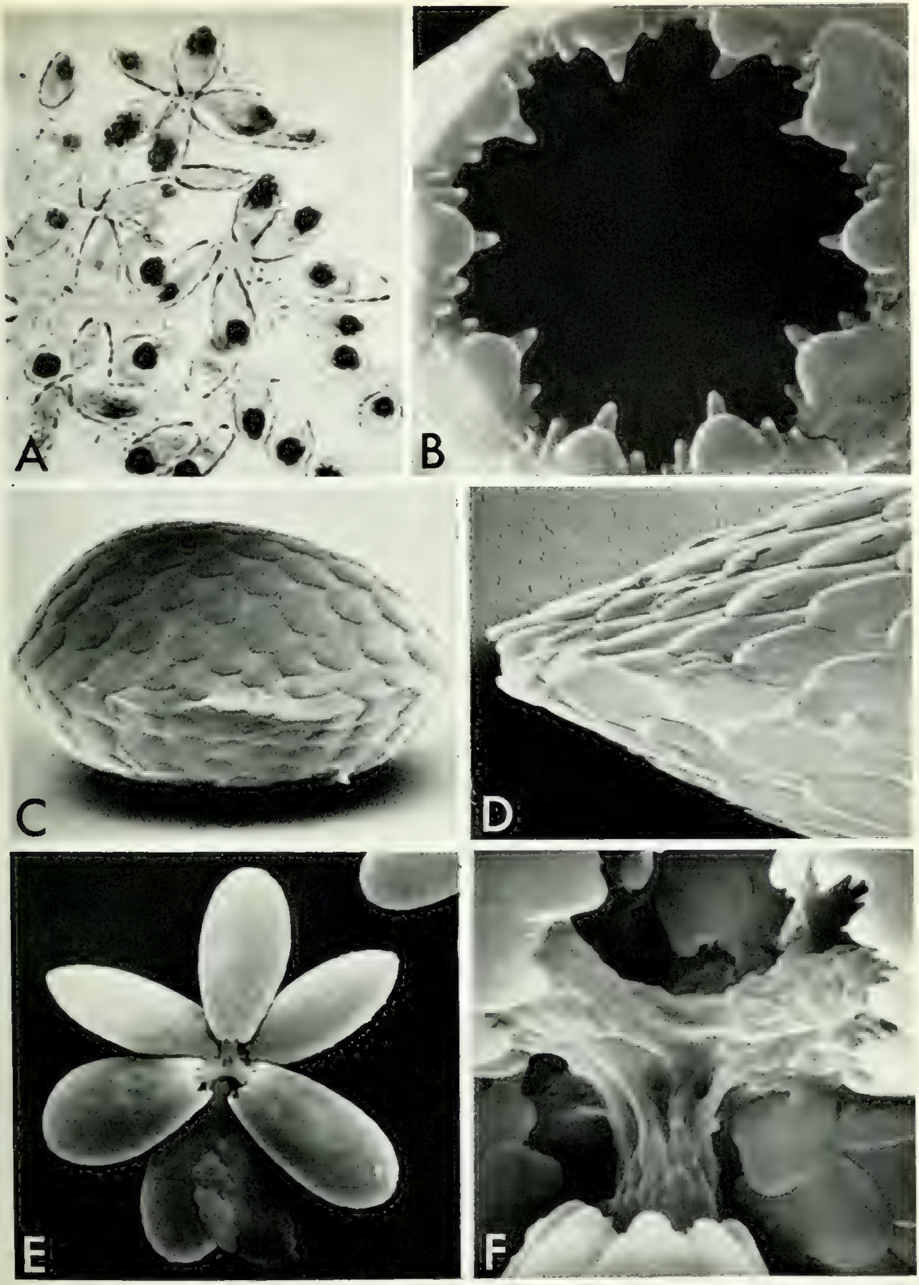


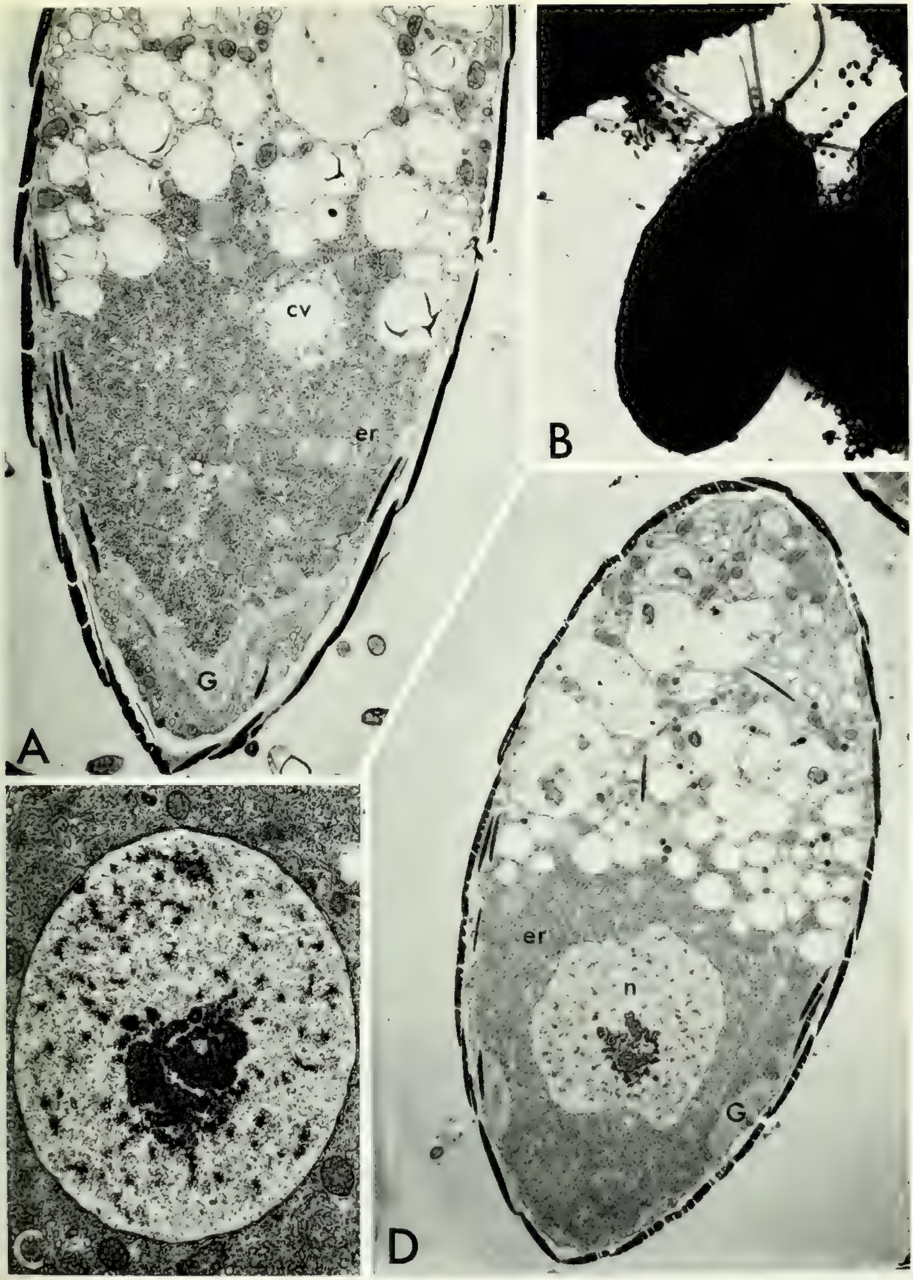
PLATE 3

A. Longitudinal section showing the position of contractile vacuole (cv), Golgi apparatus (G) and endoplasmic reticulum (er); note the structureless appearance of the 'pigment zone'. × 5,760

B. Direct preparation of whole animal showing the arrangement of pseudopodia. × 1,400

C. Transverse section of normal nucleus, with prominent electron-dense central nucleolus. × 8,640

D. Longitudinal section of an unusually shaped nucleus (n) lying in the dense endoplasmic reticulum (er); Golgi apparatus (G). × 4,320


cv
er
G
A
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C
er
n
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D

PLATE 4

A. Glutaraldehyde fixed, unstained longitudinal section to illustrate the arrangements of siliceous plates in nuclear region ; note that the ' pigment zone ' does not contain electron-dense material. × 4,200

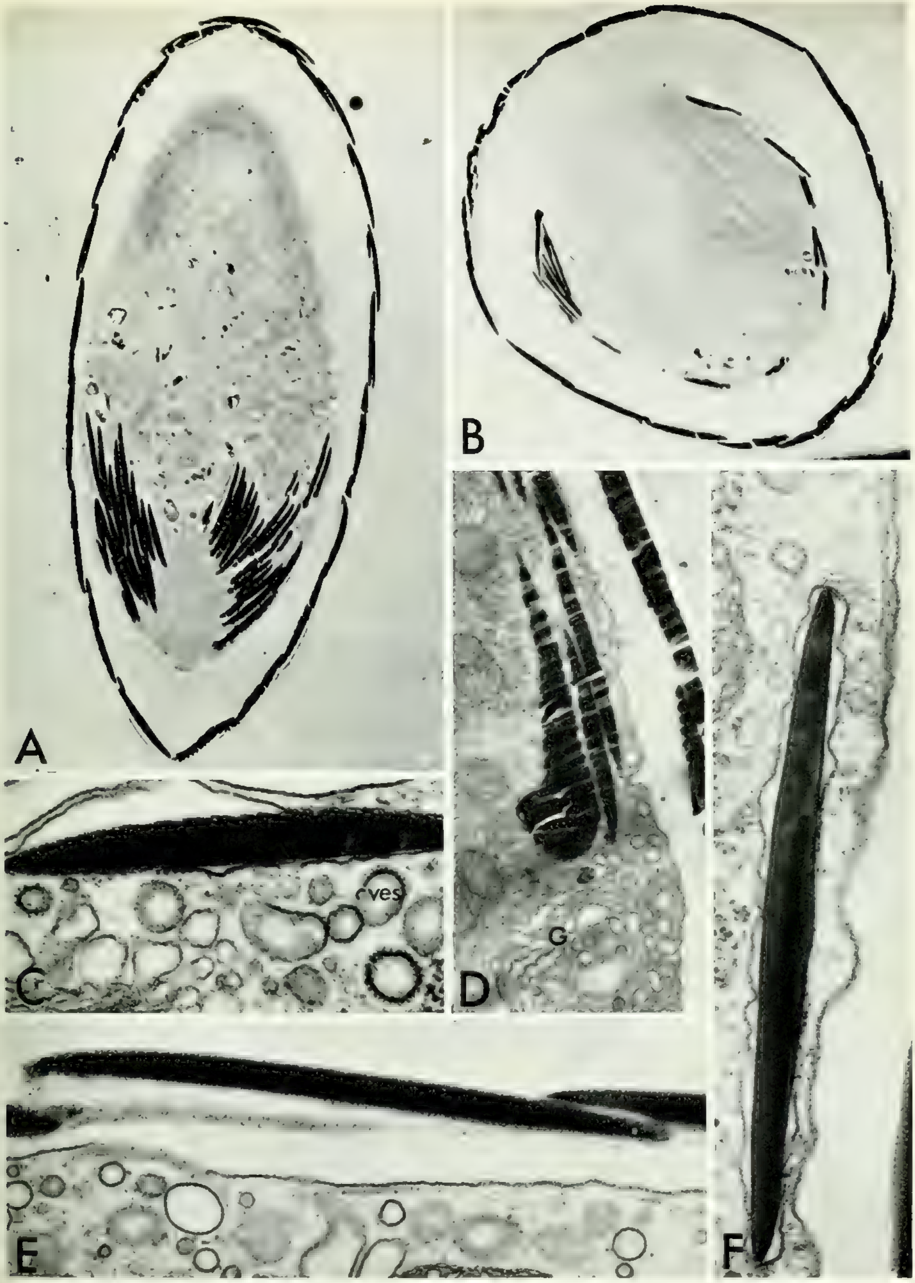
B. Glutaraldehyde fixed, unstained transverse section showing the peripheral arrangement of reserve plates. × 4,200

C Section through part of Golgi apparatus, bottom left, showing proximity of coated vesicles (cves) and reserve shell-plate. × 44,400

D. Section showing a reserve apertural-plate in close proximity to the Golgi apparatus (G) ; note fracture lines apparently caused by sectioning procedures. × 15,570

E. Siliceous plate showing the associated amorphous (?) organic cement. × 28,350

F. Reserve shell-plate in membrane-bound vesicle. × 56,700


A
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ves
C
G
D
E
F

PLATE 5

A. Vesicle containing organic cement discharging into shell cavity. × 37,800

B. Vesicles containing cement material lying adjacent to plasmalemma. × 56,700

C. Section stained with silver methenamine, showing positive reaction by organic cement vesicles for polysaccharide. × 7,780

D. Cement body showing regularly striated structure. × 60,400

E. Banded organic cement body with dense polar staining. × 56,700

F & G. Examples of mitochondrial degeneration from ' rosette ' specimens. × 28,350

H. Section through apertural region of a specimen from a ' rosette ' group showing position of cement containing vesicles ; note the concentration of microfilaments (arrowed). × 5,760

PLATE 5

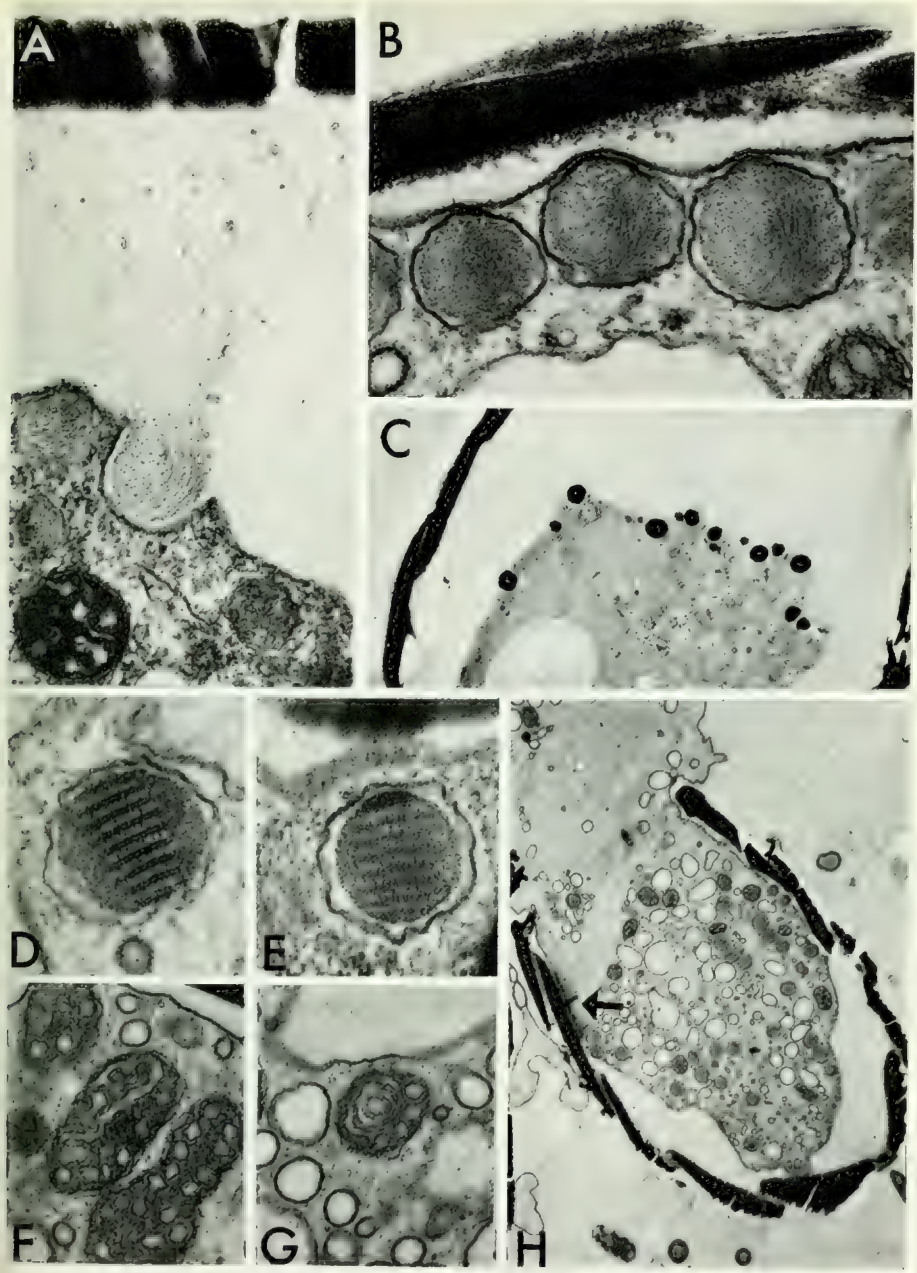

PLATE 6

Sections from specimens joined in ' rosette ' formation : A. Section through group of animals showing the extent to which cytoplasm protrudes beyond the shell ; note the bacteria (b) being engulfed. × 2,800. B. Transverse section showing the position of pellicular microtubules (pmt) and cement-containing bodies (cm) ; the arrows indicate concentrations of microfilaments. × 7,780. C. Section through apertural region showing microfilaments oriented in straight lines. × 30,090. D. Section of exocytoic vesicle containing siliceous shell. × 30,090.

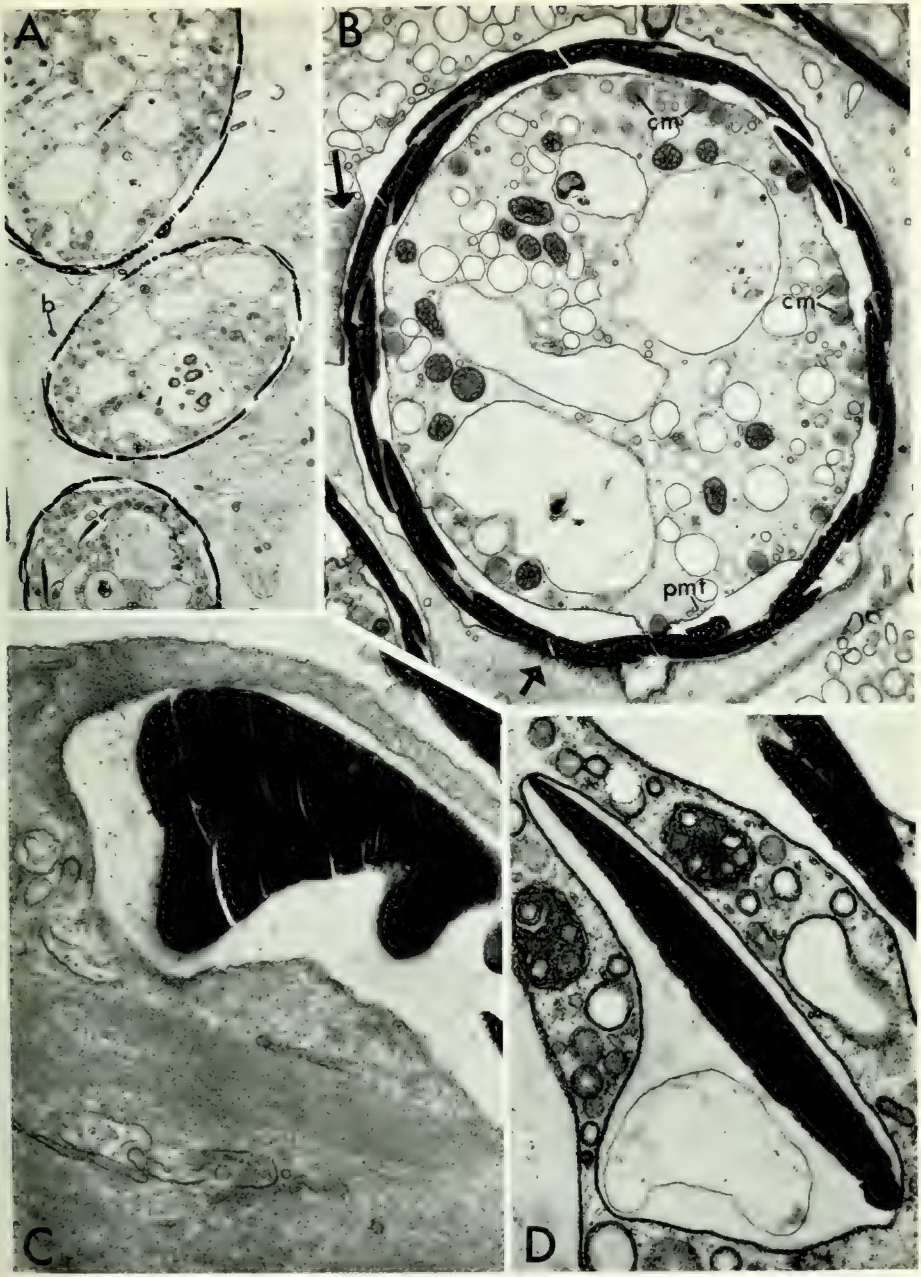
A
b
B
cm
cm
pmt
C
D

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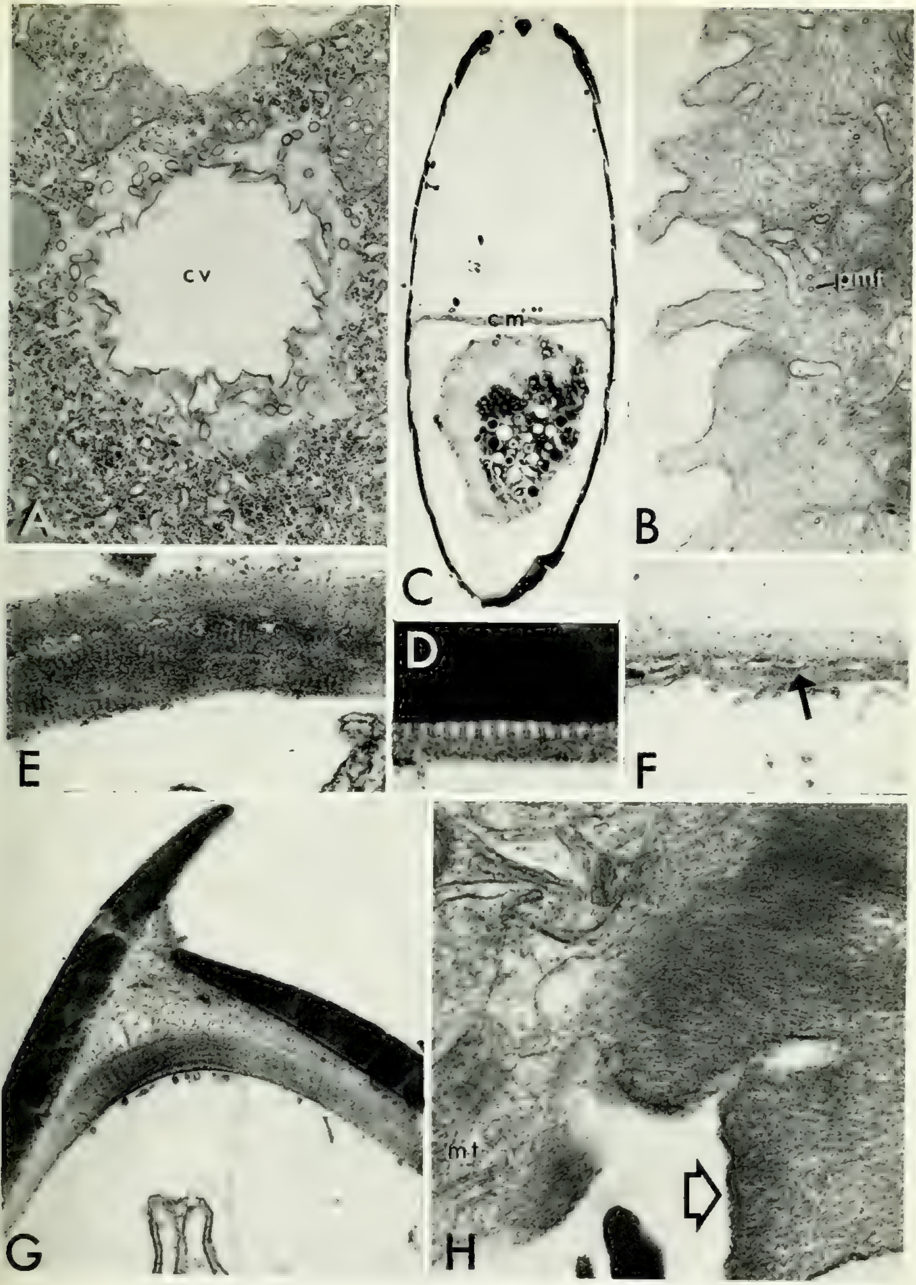
PLATE 7

A. Section through contractile vacuole (cv) and spongiome. × 18,900
B. Section of cyst plasmalemma showing invaginations and pellicular microtubules (pmt). × 29,700
C Longitudinal section showing position of cyst membrane (cm) and cytoplasm. × 2,800
D Striated cyst membrane on inside of shell-plate. × 55,200
E Section through mature cyst membrane showing striated structure. × 30,090
F. Section through early cyst membrane showing unconnected membrane (arrowed). × 56,700
G Junction of shell-plates at posterior of animal with unusually large amount of organic cement behind the plates and cyst membrane; note the striated cyst membrane. × 37,800
H. Microfilaments curving around apertural-plate; note the internal microtubules (mt) and concentration of microfilaments at the external surface of the plate (arrowed). × 37,800


A
cv
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mt

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P. H. GREENWOOD

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LONDON: 1973

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BY

PETER HUMPHRY GREENWOOD

Pp. 139–242 ; 40 *Text-figures*

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A REVISION OF THE *HAPLOCHROMIS* AND RELATED SPECIES (PISCES : CICHLIDAE) FROM LAKE GEORGE, UGANDA

By P. H. GREENWOOD

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INTRODUCTION

LAKE GEORGE, smallest of the African 'Great Lakes' (text-fig. 1), occupies a virtually square basin of about 270 km² area in the western Rift valley (0°55′ N to 0°05′ S, and 30°02′ E to 30°18′ E). Water depth over much of the lake rarely exceeds 2·5 m, although there are some circumscribed areas with depths of up to 4·0 m.

Most of the lake is bordered by flat savannah-bush, but to the north and east there are areas of papyrus swamp extending, albeit as narrow fingers, for some 15 km from the lake edge. The principal affluent rivers enter Lake George through these papyrus swamps. The Rivers Sibwe, Nsonge and Mubuka arise in the Ruwenzori mountains; the Mpanga, however, is a westward flowing tributary of the Katonga, a river which also flows eastward to enter Lake Victoria. The shared headwater of this river is a swamp divide (Doornkamp & Temple 1966), apparently impenetrable to all but air-breathing fishes.

Much of the shore line is simple, but there are a few deeply indented bays and one steep-sided bay formed from a volcanic crater.

Considerable areas of the lake bottom are covered by thick (*ca* 3 m) deposits of flocculent organic ooze, overlying a firm clay substrate. In some places, both in- and offshore, a sandy substrate is exposed or is but thinly overlaid by mud.

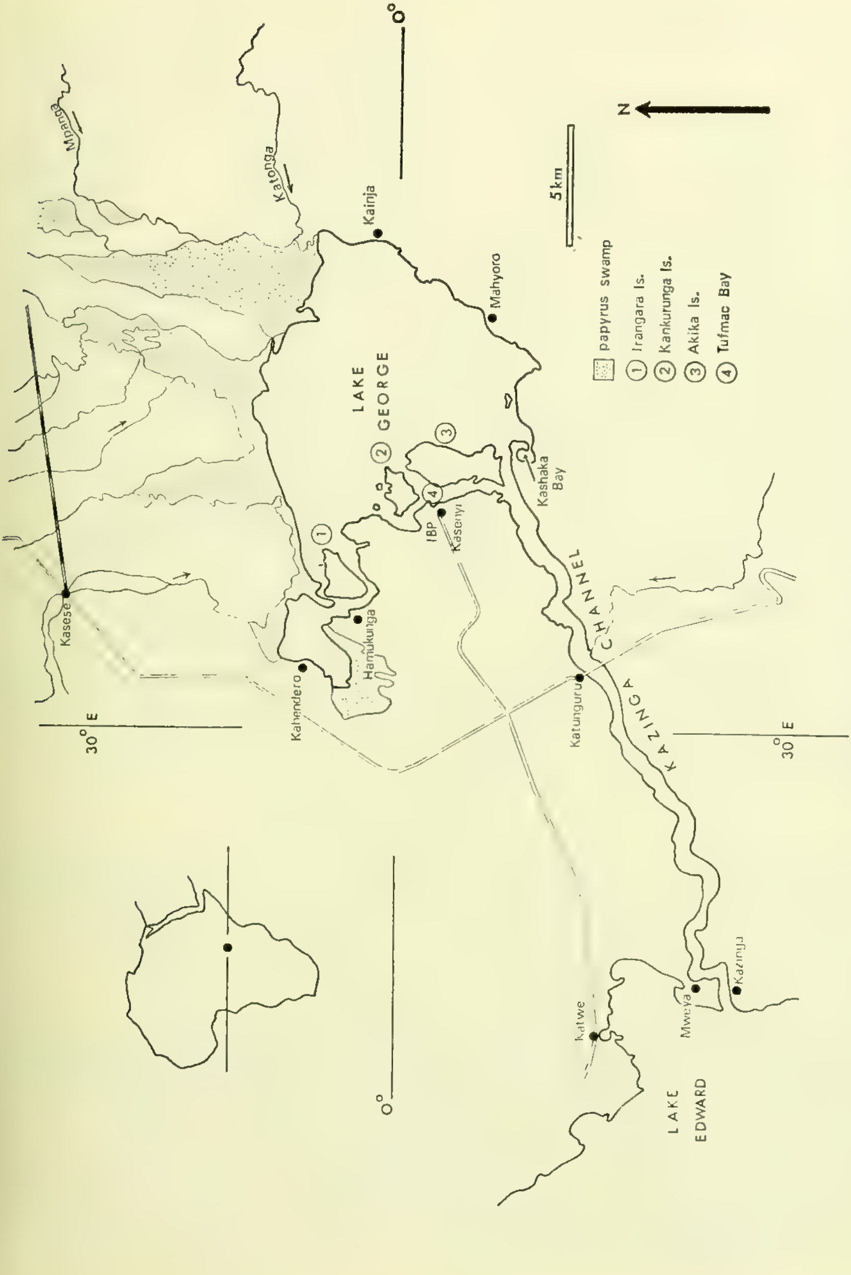
Two large islands (Kankurunga and Akika) lie close to the western lake shore; a third (Irangara Island), on the north-western shore, almost occludes the entrance to the lake's largest and most sheltered bay, Hamukunga Bay. The island shorelines are varied and include slightly indented muddy bays, short stretches of sandy beach and extensive but narrow fringes of papyrus.

For a more detailed description of the lake and a brief outline of its limnological features, reference should be made to Dunn, Burgis, Ganf, McGowan & Viner (1969).

In addition to its small size and extreme shallowness, Lake George also differs from the other 'Great Lakes' in being directly linked with another water body, Lake Edward. Connection between Lakes Edward and George is effected through the Kazinga Channel, a 36 km long, river-like passage uninterrupted by swamps or rapids. There is a definite net outflow of water from Lake George into Lake Edward but the current is slight, and on occasion, undergoes wind-induced reversal of flow, at least in the upper layers of water.

To what extent the Kazinga Channel allows an actual exchange of fishes between the lakes (or of gene flow between populations of fishes in the lakes) has yet to be determined. Certainly many species of cichlid and non-cichlid fishes are present in both lakes, and the apparent endemism of some Lake George *Haplochromis* species may well be just a reflection of inadequate collecting in Lake Edward. Nevertheless, some habitats in Lake Edward are not represented in Lake George, and it is almost certain that a few Edward species are absent from Lake George. These absentees include not only species from deep-water habitats but also several from inshore habitats as well. Their absence from Lake George is hardly attributable to inadequate sampling because that lake has been intensively collected during the past six years.

Fairly comprehensive fish collections have been made recently along the whole length of the Kazinga Channel (*see* Appendix II). These collections indicate that the *Haplochromis* species of the channel are exclusively those common to both Lake Edward and Lake George. Surprisingly, even as close to Lake Edward as the Mweya Peninsula none of the inshore-living and apparently endemic Lake Edward species was found in the channel. Clearly, detailed ecological studies will have to be made (particularly at the Lake Edward end of the channel) before this situation is understood. For the moment, however, there seem to be good *a priori* grounds for believing that, for many species, there is continuity of populations between the lakes.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0°
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Mahyoro
LAKE GEORGE
①
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③
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Kasese
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Hamukunga
IBP
Kasenyi
Kashaka Bay
CHANNEL
KAZINGA
Katunguru
30° E
5km
N
▨ papyrus swamp
① Irangara Is.
② Kankurunga Is.
③ Akika Is.
④ Tufmac Bay
Kazinga
Mweya
Katwe
LAKE EDWARD

FIG. 1. Lake George and its major affluent rivers. Inset shows geographical position of the lake. Modified after Dunn *et al.* (1969).

Little precise information is available on the age of Lake George in its present form, or of its past history. Dating of lake core samples suggests that the deposits are in the order of 3500 years old (unpublished data from International Biological Programme research). The general geological history of the area (as outlined by Doornkamp & Temple 1966) indicates, however, that a lake occupied the present George–Edward basin from at least the later Middle Pleistocene until the later Pleistocene. It seems possible, therefore, that an earlier Lake George ' disappeared ' (through causes unknown) and was later recreated, presumably from the then existing Lake Edward. Certainly the fishes indicate derivation from a common source at some recent time.

Ideally, any revision of the Lake George *Haplochromis* species should be combined with a revision of the Lake Edward species. For a variety of reasons the ideal could not be met ; in particular it has not been possible to get additional material from all areas of Lake Edward. A rather pragmatic reason for undertaking a revision of the Lake George species alone and at this time was the need to provide information for the International Biological Programme team working on the lake (*see* Dunn *et al.* 1969). Since 1967 a group of British and Ugandan biologists has been studying various levels of productivity in Lake George. Three team members have, at different times, been concerned with the ecology and distribution of the *Haplochromis* species. Since their results will be published in detail, I have concentrated, in this paper, on the taxonomic problems involved. Only brief outlines of the species' biology are given, and these may be modified in the light of later research by the I.B.P. team.

Because specimens and data for Lake George *Haplochromis* species now outnumber those available for Lake Edward, it seemed inadvisable to attempt any interlake comparisons between samples from species occurring in both lakes. As a general impression, however, I suspect that interpopulation differences will eventually be detected.

MATERIALS AND METHODS

Haplochromis species from Lake George were poorly represented in the British Museum (Natural History) collections. Consequently, most of the material on which this paper is based is that obtained during the I.B.P. investigation of the lake. In the only previous revision (Trewavas 1933), Lake George specimens were treated together with fishes from Lake Edward.

Because I have not studied Lake Edward fishes in any detail, the synonymies given below include, with few exceptions, only those Lake George specimens actually mentioned in Trewavas' (*op. cit.*) paper. Where necessary, however, I have included some Lake Edward specimens. For example, this has been essential when selecting certain lectotypes, or where a misidentification is corrected and, if not included in a synonymy, could lead to zoogeographical misunderstanding.

Most of the data on live coloration, distributions and breeding habits were collected personally during several visits to the lake. A lot of this information has been supplemented and refined by the observations of Dr Ian Dunn and Mr James

Gwahaba, the fish biologists of the I.B.P. team. Both these workers have given unstintingly of their time and information, and I am extremely indebted to them.

Measurements used in describing the species are those I have employed in other papers on *Haplochromis* species, viz. :

Standard length : measured directly[1] from the snout tip (including the premaxilla) to the posterior margin of the hypural bones (located by bending the caudal fin at right angles to the body's long axis).

Head length : measured directly[1] across the head from snout tip to the most posterior point on the opercular bone.

Preorbital depth : is the greatest depth of the first infraorbital bone (= lachrymal bone).

Interorbital width : is the least distance between the bony (frontal) margins of the orbit.

Snout length : measured directly[1] from the snout tip (i.e. the premaxillary symphysis) to the anterior orbital margin.

Eye diameter : is the greatest diameter of the bony orbit in the horizontal plane.

Cheek depth : is the greatest depth of the muscular part of the cheek (even when this extends below the scale rows) and is measured vertically.

Lower jaw length : is measured directly[1] from the dentary symphysis to the posterior margin of the articular bone (located by opening the lower jaw and finding its point of articulation).

Upper jaw length : is measured directly[1] from the premaxillary symphysis to the posterior margin of the maxilla.

Caudal peduncle length : is taken from the posterior margin of the hypurals to a vertical projected from the insertion of the last anal ray. *Peduncle depth* is the least depth.

A character I have used for the first time concerns the so-called *pseudorakers* on the first gill arch. These structures lie on the anterior (i.e. upper) face of the arch, between the inner and outer rows of true gill rakers. Pseudorakers are localized thickenings of the tissue covering the arch. In gross appearance they resemble true gill rakers, but unlike those structures they lack a bony central core.

Vertebral counts do not include the fused first preural and ural vertebrae (which support the parhypural and hypurals).

Haplochromis elegans Trewavas, 1933

(Text-figs. 2 & 3)

Haplochromis nubilus (part) : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 329 (specimens BMNH reg. nos. 1933.2.23 : 288–295 from Lake George).

H. elegans (part) Trewavas, *op. cit.* : 332 (3 paralectotypes, reg. nos. 1933.2.23 : 387–389, supposedly from Lake George, and 4 other specimens, 1933.2.23 : 390–393, also from that lake).

NOTE ON THE SYNONYMY. According to Trewavas (1933), three *H. elegans* syntypes (all females) are from Lake George, the other syntypical material being from Lake

---

[1] In a direct measurement, one tip of the dividers or calipers is placed at one of the points specified and the other tip is placed on the second point; the distance measured may thus run across the long axis of the fish (as, for example, in snout and head lengths).

Edward. I have examined the three syntypes (reg. nos. 1933.2.23 : 387–389) and agree with Trewavas' identification. However, the bottle label, and the Museum register, give the locality for these fishes as Lake Edward and not Lake George.

Trewavas (*op. cit.*) also refers seven specimens from the hypodigm (reg. nos. 1933.2.23 : 390–395) to this species, giving their localities as Worthington's (1932) stations 522 (Lake Edward) and 613 (Lake George). Six fishes (reg. nos. 1933.2.23 : 390–395) are in a bottle now labelled ' Lake George ' but without any station number quoted. I take these to be the fishes from station 613. Of these specimens, three are referable to *H. elegans.*

The *lectotype*, an adult male 65·5 mm standard length (BMNH 1933.2.23 : 381), is from Lake Edward.

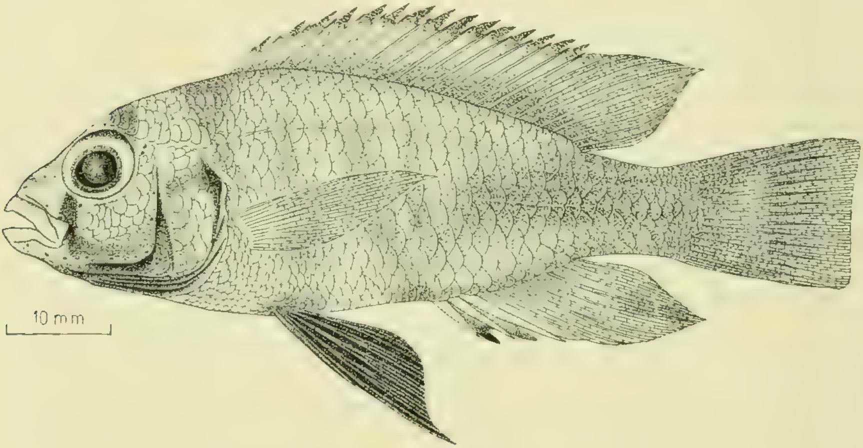

FIG. 2. *Haplochromis elegans.* Lake George specimen ; a male.

DESCRIPTION. Based on 34 specimens, 58·0–72·5 mm standard length (but not including the lectotype since it is from Lake Edward).

Depth of body 35·7–40·8 (mean, M = 37·6) per cent of standard length, length of head 32·2–35·4 (M = 33·7) per cent. Dorsal profile of head gently decurved or straight, sloping at about 35° to the horizontal ; dorsal margin of eye not entering the line of the profile, but clearly below it.

Preorbital depth 11·8–16·5 (M = 14·5) per cent of head, showing very slight positive allometry. Least interorbital width 21·9–27·3 (M = 24·2) per cent of head, length of snout 25·6–32·5 (M = 28·4) per cent, 0·8–0·9 of its breadth. Eye diameter 28·0–37·0 (M = 33·5) per cent of head (not showing clear-cut allometry in the size range examined), depth of cheek 18·2–24·4 (M = 20·8) per cent.

Caudal peduncle 13·8–18·7 (M = 16·2) per cent of standard length, 1·2–1·5 (modal range 1·2–1·3) times as long as deep.

Mouth horizontal or very slightly oblique ; lips somewhat thickened. Length of upper jaw 28·6–34·0 (M = 30·3) per cent of head, length of lower jaw 35·0–40·2

(M = 37·9) per cent, 1·3–1·8 (mode 1·4) times as long as broad. Posterior tip of maxilla reaching the vertical through the anterior orbital margin, but not quite reaching this level in a few specimens.

Gill rakers variable in form but usually rather stout, the lower 1 or 2 greatly reduced ; 8 or 9 rakers in the outer row on the lower part of the first gill arch. No pseudorakers are developed between the inner and outer rows of gill rakers on this arch.

Scales. Ctenoid ; lateral line with 30 (f.2), 31 (f.15), 32 (f.15), 33 (f.1) or 34 (f.1) scales ; cheek with 2 or 3 (mode) rows. Five to 6½ (mode 5½) scales between the upper lateral line series and the dorsal fin origin, 6–8 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.2), 15 (f.24) or 16 (f.8) spinous and 8 (f.1), 9 (f.21) or 10 (f.12) branched rays. Caudal subtruncate, scaled on its basal half, or a little beyond. Pectoral 26·6–33·6 (M = 30·3) per cent of standard length, 80·0–97·8 (M = 90·0) per cent of head. Pelvics with the first two rays produced, especially in adult males.

Teeth. The *outer row* of teeth in both jaws (text-fig. 3) is composed principally of relatively stout, well-spaced, unequally bicuspid teeth ; anteriorly in the lower jaw, the teeth are implanted so as to slope forward at a slight angle.

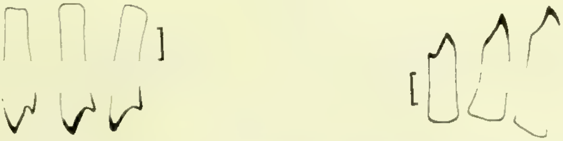

FIG. 3. *H. elegans.* (Left). Premaxillary teeth, left side, viewed from a point slightly anterior of lateral. The teeth are from an anterolateral position in the jaw. (Right). Dentary teeth (right side), lateral in position. Viewed laterally. Scale = 0·25 mm.

The major cusp is isoscelene in outline (*see* text-fig. 3) and very slightly incurved ; the neck of the tooth is slightly flattened in cross-section. Some teeth in each jaw have one margin of the major cusp partly flattened from below the tip so that it appears as a narrow step-like flange adjacent to the minor cusp (*cf. H. aeneocolor* where the flange is present on most teeth and is more obvious).

Posteriorly in the upper jaw there may be from 1 to 5 unicuspid and dagger-shaped teeth ; less often these posterior teeth are tricuspid.

There are 34–42 (mean = 38) teeth in the outer premaxillary row.

The inner rows (usually 2, less commonly 3 in the upper jaw, and 2 or 3 in the lower) are composed of small tricuspid teeth, often irregularly arranged (particularly in the upper jaw).

OSTEOLOGY. The *neurocranium* of *H. elegans* is typically that of a generalized *Haplochromis* species (*see* Greenwood 1962), although the preorbital profile is a little less decurved.

The lower *pharyngeal bone* is fairly stout, with its dentigerous area 1·1–1·2 times broader than long. The teeth are fine, cuspidate and compressed and are arranged in 24–26 rows. Teeth in the two median rows are somewhat coarser than the others.

Vertebral counts for the 30 specimens radiographed are : 28 (f.3), 29 (f.22) or 30 (f.5), comprising 12 (f.5), 13 (f.24) or 14 (f.1) abdominal and 15 (f.2), 16 (f.20) or 17 (f.8) caudal elements.

COLORATION IN LIFE. *Adult males* : ground colour smokey grey overlying bluish-silver. Snout, lips and cheek with a livid iridescence. Belly and branchiostegal membrane dark cinder grey. Dorsal fin with the spinous part sooty, the inter-spinous membrane generally darkest ; lappets black but with a narrow red streak (or spot) at the tip. Soft dorsal with maroon streaks between the rays. Caudal fin with maroon spots and blotches between the rays, and a suffuse maroon flush around the fin margin. Anal dark hyaline (or faintly grey) often dusky at its base and with a pinkish-maroon border. The pelvics are black.

Females : ground colour sandy green shading to silvery white on the belly and lower flanks. All fins yellowish-green. Because female *H. elegans* are not immediately identifiable in the field, these ' live ' colours are in fact ' post-mortem ' colours and should not be considered at all precise.

COLORATION IN PRESERVED SPECIMENS. *Adult males* : ground colour variable but basically grey-brown ; belly and chest dusky, as are, sometimes, the flanks. The flanks are generally crossed by 3–6 faint vertical bars. The branchiostegal membrane is black. Cephalic markings comprise a distinct lachrymal stripe, two bars across the snout and a broader bar immediately behind the orbits ; in many specimens there is an even broader, but fainter, bar or blotch transversely across the nape. The lower part of the cheek and the vertical limb of the preoperculum are sometimes dusky.

The dorsal fin is dusky, with darker streaks between the spines and rays, or the latter region maculate. Anal fin dusky or indistinctly maculate. Caudal with a dark central area and a light marginal zone. Pelvics are black, and the pectorals hyaline.

Females have a greyish-yellow ground coloration, and sometimes very faint traces of 3–6 vertical bars on the flanks. On the head there are slight indications (sometimes just a darker area) of two bars across the snout, and a lachrymal stripe. All the fins are hyaline, the dorsal usually darker than the others ; the caudal is often maculate.

ECOLOGY. *Habitat. Haplochromis elegans* is essentially a species of the inshore regions of the lake, especially near papyrus shores or where the bottom is sandy. It rarely occurs in open-water localities or in shallow places where the substrate is mud.

Food. Mostly chironomid larvae, although emergent aquatic Diptera are also eaten when available.

Breeding. Haplochromis elegans is a female mouth-brooder. All specimens, of both sexes, within the size range studied are adult ; females appear to reach a larger size than do males. In the 15 sexually active females examined, 11 have the right ovary noticeably larger than the left, 2 have the ovaries equally developed, and 2 have the right ovary a little larger than the left one.

Distribution. Lakes Edward and George, and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Within Lake George, *H. elegans* most closely resembles *H. aeneocolor* (*see* p. 150), both morphologically and in its habitat preferences. Adult males of the two species are readily distinguished by their coloration, but females and preserved specimens are differentiated chiefly by the fewer and somewhat stouter teeth of *H. elegans* (32–42, M = 38, *cf.* 40–58, M = 48 in *H. aeneocolor*), the slightly procumbent anterior dentary teeth of *H. elegans*, the well-developed flange on the major cusp of most teeth in *H. aeneocolor* (*see* p. 151), the shorter upper jaw of *H. elegans* (28·6–34·0, M = 30·3 per cent of head, *cf.* 30·0–37·8, M = 34·9 per cent) and the shorter lower jaw of *H. elegans* (35·0–40·2, M = 37·9 per cent of head, *cf.* 38·0–44·0, M = 41·0 per cent in *H. aeneocolor*). In life the lips of *H. elegans* appear thicker than those of *H. aeneocolor*, but this distinction is less obvious in preserved material.

Haplochromis elegans shows few specializations in its dental or cranial anatomy, and must be ranked amongst the 'generalized' *Haplochromis* species. Outside the Lake Edward–Lake George species complex it resembles *H. pallidus* (Blgr.) of Lake Victoria (*see* Greenwood 1960). From *H. pallidus*, *H. elegans* differs in its adult male coloration, some morphometric characters (e.g. having a shorter snout) and in its overall morphology. The significance of this apparent resemblance will be discussed elsewhere (p. 230); however, it should be noted that the resemblance between *H. elegans* and *H. pallidus* cannot be shown to be more significant than that existing between it and species of the *H. bloyeti* complex (*see* Greenwood 1971).

Trewavas (1933) compared *H. elegans* with *H. cinereus* (Blgr.) of Lake Victoria, but this comparison is no longer valid now that we have a clearer concept of *H. cinereus* (*see* Greenwood 1960). In fact, *H. cinereus* shows some specialized characters (its dentition for one). These specializations would not be apparent in 1933, because at that time '*H. cinereus*' was a dumping ground for several of the generalized Lake Victoria species.

Resemblances which I noted between *H. elegans* and *H. velifer* Trewavas of Lake Nabugabo (Greenwood 1965b) are somewhat diluted by the greater amount of information now available on *H. elegans*. For example, the teeth of *H. elegans* (at least in Lake George populations) have a more acutely pointed cusp, and there are fewer teeth in the outer premaxillary row. There is, of course, a marked difference in the male breeding coloration of the two species.

Diagnostic problems arising in connection with *H. elegans* and species at present known only from Lake Edward (and then very imperfectly known) are virtually identical with those discussed in relation to *H. aeneocolor* on page 153.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 166–167	N.E. lake shore (papyrus)
1972.6.2 : 168–171	Papyrus shore off I.B.P. Laboratory
1972.6.2 : 172–177	Kankurunga Island

1972.6.2 : 178–179	Kankurunga Island
1972.6.2 : 180–182	Kankurunga Island
1972.6.2 : 183–206	Kankurunga Island
1972.6.2 : 207–224	Kankurunga Island
1972.6.2 : 225–230	Kankurunga Island
1972.6.2 : 231–236	Kankurunga Island
1972.6.2 : 237–238	Akika Island
1972.6.2 : 239–243	Akika Island
1972.6.2 : 244–260	Akika Island
1972.6.2 : 261–272	I.B.P. Jetty
1972.6.2 : 273–285	Kashaka Bay
1972.6.2 : 286–291	Tufmac Bay
1972.6.2 : 292	Close to shore (muddy)

Haplochromis aeneocolor sp. nov.

(Text-figs. 4 & 5)

Haplochromis nubilus (part) : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*) **38** : 329 (4 specimens, BMNH reg. nos. 1933.2.23 : 296–299).

HOLOTYPE. A male, 68·0 mm standard length, BMNH reg. no. 1972.6.2 : 43.

The specific name refers to the brassy appearance of adult males.

DESCRIPTION. Based on 36 specimens (including the holotype), 58·0–75·0 mm standard length.

Depth of body 35·7–41·1 (M = 37·7) per cent of standard length, length of head 32·0–36·8 (M = 34·5) per cent. Dorsal profile of head straight or slightly concave, sloping fairly steeply at *ca* 35°–40° with the horizontal ; dorsal margin of orbit not entering the line of the profile but distinctly below it.

Preorbital depth 12·0–18·2 (M = 14·6) per cent of head (not showing any clear-cut allometry), least interorbital width 22·7–29·3 (M = 25·5) per cent, snout length 26·7–31·8 (M = 28·8) per cent, 0·8–1·0 (mode 0·9) of its breadth. Eye diameter 28·6–35·0 (M = 31·4) per cent of head (showing no obvious allometry), depth of cheek 19·0–25·0 (M = 22·8) per cent.

Caudal peduncle 12·9–17·4 (M = 15·3) per cent of standard length, 1·2–1·5 (modal range 1·2–1·3) times as long as deep.

Mouth angle ranging from horizontal to slightly oblique ; lips somewhat thickened. Length of upper jaw 30·0–37·8 (M = 34·9) per cent of head, lower jaw 38·0–44·0 (M = 41·0) per cent of head, 1·5–2·1 (modal range 1·6–1·8) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even to a vertical through the anterior margin of the pupil.

Gill rakers of various shapes, from short and stout to relatively slender ; the lower 1 or 2 rakers on the first gill arch are greatly reduced, the upper 2 or 3 often flattened. There are 8 or 9 rakers on the lower part of the first arch.

Pseudorakers are poorly developed.

Scales. Ctenoid ; lateral line with 30 (f.11), 31 (f.18), 32 (f.4) or 33 (f.1) scales, cheek with 3 (rarely 2) rows. Five to 6½ (mode 5½) scales between the lateral line and the dorsal fin origin, 6 (mode) or 7, rarely 5½ or 5, between the pectoral and pelvic fin bases.

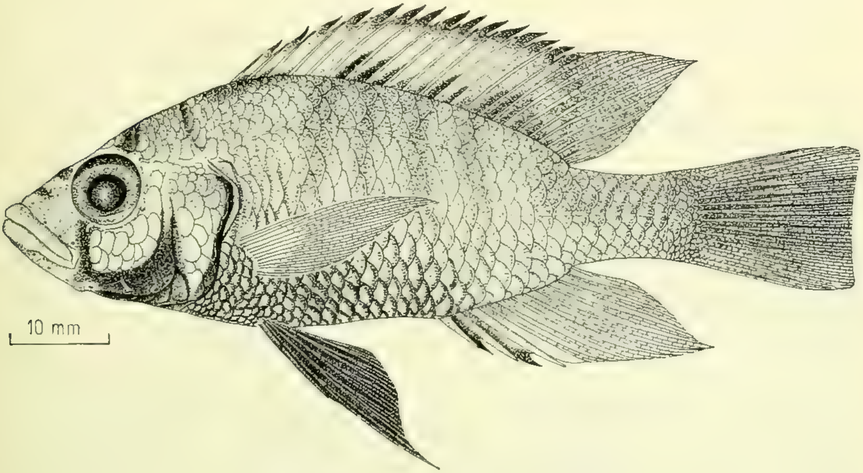

FIG. 4. *Haplochromis aeneocolor.* Holotype.

Fins. Dorsal with 14 (f.3), 15 (f.31) or 16 (f.2) spinous and 8 (f.3), 9 (f.25) or 10 (f.8) branched rays. Anal with 3 spines and 7 (f.1), 8 (f.9), 9 (f.20) or 10 (f.6) branched rays. Caudal subtruncate, scaled on its basal half. Pectoral 27·0–31·7 (M = 28·9) per cent of standard length, 73·8–93·5 (M = 84·5) per cent of head. Pelvics with the first and second rays produced (the first markedly so), and relatively longer in adult males than in females.

Teeth. The *outer teeth,* although basically of the generalized, unequally bicuspid type, are nevertheless rather distinctive. This is due to the presence of a well-developed, thin flange on that margin of the outer cusp which is adjacent to the minor cusp (*see* text-fig. 5). Few individuals fail to show flange development on at least the majority of anterior and lateral teeth in both jaws. The flange can be so well developed that the tooth seems to have an expanded and obliquely sloping major cusp (i.e. to be like the teeth of *H. limax, see* p. 168). Usually the flange is thin and almost transparent, so that there appears to be a dividing line between it and the more substantial body of the cusp itself. Although the flange may be continuous with the occlusal (i.e. distal) part of the cusp (thereby simulating an *H. limax*-like tooth) it is generally confined to the proximal half or two-thirds of the cusp. In this way a distinct step is developed between the flange and the occlusal tip of the cusp.

Apart from the flange, outer teeth in *H. aeneocolor* are typical bicuspids, with the major cusp having the outline of an isosceles triangle rather than of an equilateral one. The minor cusp is well developed, but its tip is not very acute. The crown of an outer tooth has virtually no incurvature, and the neck is a slightly compressed cylinder.

The posterior 1–4 upper teeth are either compressed tricuspids or are unicuspid and caniniform.

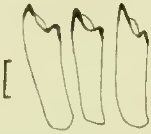

FIG. 5. *H. aeneocolor.* Dentary teeth (left side), lateral in position. Viewed laterally. Scale = 0·25 mm.

There are 40–56 (mean 48) teeth in the outer row of the upper jaw.

In a few specimens, all the outer teeth in the lower jaw are unicuspid, but the upper teeth retain a typical bicuspid form.

The *inner teeth* in both jaws are small, compressed and tricuspid, and are arranged in 2 or 3 (rarely 4) series in the upper jaw, and in 2 (rarely 1 or 3) series in the lower jaw.

OSTEOLOGY. The *neurocranium* is of the typical generalized *Haplochromis* type (*see* Greenwood 1962), but with the preorbital profile slightly straighter.

The *lower pharyngeal bone* is moderately stout, its dentigerous area equilateral or slightly broader than long. The teeth are fine, compressed and cuspidate, and are arranged in *ca* 24–26 rows ; the median teeth are not noticeably larger or coarser than those of the lateral rows.

Vertebral counts in the 16 fishes examined are 27 (f.1), 28 (f.7) and 29 (f.8), comprising 12 (f.6) or 13 (f.10) abdominal and 15 (f.4), 16 (f.11) or 17 (f.1) caudal elements.

COLORATION IN LIFE. *Adult males* : the flanks, lateral aspect of the chest and belly, lower part of the head, the branchiostegal membrane and the lips are dark sulphurous yellow, with an orange overlay on the operculum. The rest of the flank (i.e. the posterior part) and the caudal peduncle are yellowish-green with a faint bluish overlay, and the ventral aspect of the chest is sooty. The dorsal body surface is dull bronze posteriorly, becoming purple above the flanks, and crimson anteriorly. The snout and anterior dorsum of the head are puce.

The overall colour impression gained from a newly caught male is one of brassyness, despite the various colour elements described above.

The dorsal fin is dark hyaline on the spinous part (the lappets black), but lighter on the soft part where the margin is crimson. The anal fin is hyaline over the basal third of the soft part, but with the spines and distal two-thirds of the soft part pinkish-crimson ; the ocelli are orange-yellow. The caudal fin is pinkish to red, the colour intensified on the ventral third of the fin and at its posterior angle. The pelvic fins are black, the pectorals hyaline.

Male coloration is difficult to describe adequately because the intensity of the various colours is variable and changes rapidly after the fish is removed from water. Some fishes, for example, appear almost black a short while after capture.

PRESERVED COLORATION. *Males*: the ground colour is essentially like that described for *H. elegans* (*see* p. 148), but in *H. aeneocolor* the dark ventral pigment is more extensive; in some individuals it covers the entire caudal peduncle and the flanks to a level just below the upper lateral line. Cephalic markings are identical in both species.

The dorsal fin is dusky to black; if dusky, the pigment is often concentrated basally so that this region of the fin is almost black. The caudal is more or less uniformly dark, except for hyaline areas on the ventral and posteroventral margin. The anal varies from grey to dusky; the area over the spines is generally black. The pelvic fins are black, the pectorals hyaline.

Females have a greyish-silver to greyish-yellow ground colour; the head shows very faint traces of two transverse bars across the snout and an ill-defined, short, lachrymal stripe or streak. The dorsal fin has dark streaks between the rays, especially on the spinous part. The caudal is maculate, usually weakly so, and with the spots most obvious on the centre of the fin; a few specimens have intense maculae distributed over most of the fin. The anal is hyaline as are the pelvics (which may be faintly dusky).

ECOLOGY. *Habitat.* This species is particularly common near papyrus shores, and is rare elsewhere in the inshore region. Apparently it never occurs offshore.

Food. Haplochromis aeneocolor seems to be a detritus feeder since plant fragments and insect larvae are predominant elements of its gut contents. Adult insects are, however, also eaten.

Breeding. Haplochromic aeneocolor is a female mouth brooder. Of the 10 adult females examined, the right ovary is much larger than the left in 6 individuals, slightly larger in 3 and of equal size in 1 fish.

All specimens within the size range studied are adult and there is apparently no sexual dimorphism in the maximum size attained.

Distribution. Lake George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Until more is known about most Lake Edward species (and especially those not recorded from Lake George) an adequate diagnosis for *H. aeneocolor* is difficult to compile. For example, *H. eduardii* Regan superficially resembles *H. aeneocolor* but appears to differ in having stouter, non-flanged and less acutely cuspidate teeth, a shallower body and more rounded (i.e. decurved) head profile. *Haplochromis engystoma* Trewavas (known only from the holotype and one other specimen) has dental characteristics more like those of *H. aeneocolor*, but differs in several morphometric characters, especially in its higher (2·0) eye/cheek ratio, shorter lower jaw (34·8 per cent of head) and its strongly decurved head profile. *Haplochromis vicarius* Trewavas (at least as restricted to the holotype) has an overall superficial resemblance, but differs in having obliquely cuspidate outer teeth, more rows of inner teeth and a larger eye (36·0 per cent of head); Poll (1939) has synonymized *H. vicarius* with *H. eduardii* but I doubt the correctness of this decision (*see* Appendix I).

Regrettably, in none of these comparisons could life colours be taken into account because these are unavailable for the Lake Edward species.

Considering now those species which also occur in Lake George, *H. elegans* has the closest overall and detailed resemblances with *H. aeneocolor* (*see* p. 149). Male coloration is, however, very different in the two species, and there are dental and morphometric differences as well (again, *see* p. 147). Distinguishing between females of the species is especially difficult, although in the field the more rounded head profile of *H. elegans* does give some guidance for preliminary sorting.

Haplochromis limax Trewavas shows a fairly marked resemblance to *H. aeneocolor* in its superficial morphology and there is also a certain convergence in dental morphology. This arises from the peculiar flange developed on the major cusp of outer teeth in *H. aeneocolor* (*see* p. 152). If this flange is hypertrophied, it increases the area of the major cusp and imparts to it an oblique cutting edge. However, if such teeth in *H. aeneocolor* are closely examined, the junction between flange and main body is apparent, as is a slight indentation on the cutting edge. Furthermore, the flange is much thinner (nearly transparent) than the corresponding margin of a tooth in *H. limax*. Another distinguishing feature of *H. limax* is the broader array of inner teeth, and their larger size. Again, male breeding coloration is very different in the two species.

Beyond the confines of Lakes Edward and George, *H. aeneocolor*, like *H. elegans*, resembles the generalized *Haplochromis* species of Lake Victoria, in particular *H. pallidus*. But, in the absence of any clearly defined specializations in the species involved, little significance can be attached to these resemblances. The peculiar flange formation on the outer teeth of *H. aeneocolor* is an unusual feature for *Haplochromis* but its recognition as a specialization remains to be confirmed. Certainly it is rarely manifest among Lake Victoria species, but it does occur more frequently (if only as an individual variant) amongst the species of Lakes Edward and George.

Finally, and as if to reinforce the generalized nature of *H. aeneocolor* anatomy, the resemblance between this species and *H. nubilus* (Blgr.) should be noted. *Haplochromis nubilus* is one of the anatomically and ecologically most generalized species occurring in the Victoria-Edward drainage basin (*see* p. 221), and in turn shows close affinity with the fluviatile species of east Africa. On all morphometric characters *H. nubilus* and *H. aeneocolor* cannot be separated, but male coloration is markedly distinct, the caudal of *H. nubilus* has a nearly round distal outline, flanged teeth are not found (the teeth are unicuspid in large fishes) and the dorsal head profile is more concave than in *H. aeneocolor*.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 43 (Holotype)	N.E. shore near River Mpanga mouth
1972.6.2 : 44–50 (Paratypes)	Kankurunga Island
1972.6.2 : 52–54 (Paratypes)	Kashaka Crater
1972.6.2 : 55–63 (Paratypes)	N.E. shore
1972.6.2 : 64–67 (Paratypes)	N.E. shore
1972.6.2 : 68–72 (Paratypes)	Kashaka Bay
1972.6.2 : 73–79 (Paratypes)	Kankurunga Island
1972.6.2 : 81–84	Papyrus shore off I.B.P. Laboratory

1972.6.2 : 85–103	N.E. shore
1972.6.2 : 104–111	Kankurunga Island

Haplochromis nigripinnis Regan, 1921

(Text-figs. 6 & 7)

Haplochromis nigripinnis Regan, 1921, *Ann. Mag. nat. Hist.* (9) **8** : 635.

Haplochromis nigripinnis : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 330 (refers to Lake Edward fishes only).

Haplochromis guiarti (part) : Trewavas, 1933, *op. cit.* : 340 (1 of the 3 small fishes from Worthington's (1932) stations 613 and 618, Lake George, viz. BMNH reg. no. 1933.2.23 : 476.

HOLOTYPE. A male (probably adult), 64·0 mm standard length from Lake Edward, BMNH reg. no. 1914.4.8 : 14.

DESCRIPTION. Based on 36 specimens (excluding the holotype), 50·0–68·0 mm standard length.

Depth of body 32·3–41·5 (M = 36·8) per cent of standard length, length of head 31·5–35·3 (M = 33·6) per cent. Dorsal head profile straight or gently curved, sloping at *ca* 35°–40° to the horizontal ; dorsal margin of orbit barely entering the line of the head profile.

Preorbital depth 10·0–14·6 (M = 13·0) per cent of head, least interorbital width 20·7–27·5 (M = 24·2) per cent, ratio of interorbital width to eye diameter 1·28–1·75 (M = 1·49). Snout length 24·0–30·3 (M = 27·4) per cent of head, 0·8–0·9 (rarely 1·0) its breadth ; eye diameter 33·3–40·0 (M = 35·8) per cent, with no detectable allometry ; depth of cheek 16·3–22·9 (M = 19·8) per cent.

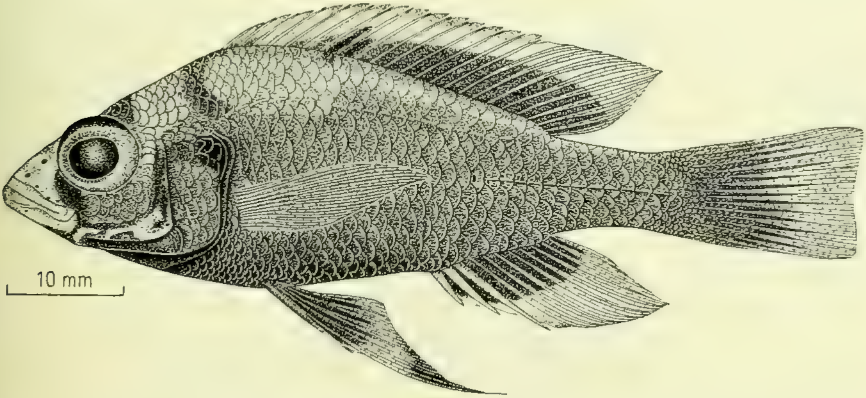

FIG. 6. *Haplochromis nigripinnis.* Lake George specimen ; a male.

Caudal peduncle 15·8–19·8 (M = 17·4) per cent of standard length, 1·3–1·8 (modal range 1·5–1·7) times as long as deep.

Mouth horizontal, lips not noticeably thickened. Length of upper jaw 30·6–36·9 (M = 34·0) per cent of head, length of lower jaw 39·0–47·5 (M = 43·6) per cent, 1·8–2·2 (modal range 1·9–2·0) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even to one through the anterior margin of the pupil.

A noticeable feature of the snout in *H. nigripinnis* is the size of the anterior opening to the nasal laterosensory canal. The opening is as large as (or almost as large as) the nostril. In most other *Haplochromis* species from Lake George (and apparently Lake Edward also) the opening to this canal is much smaller than the nostril, and is often difficult to locate.

The intestine in *H. nigripinnis* is long (*ca* 2–2½ times total length) and much coiled on itself.

Gill rakers on the first arch are, except for the reduced lower 1–3 and the occasional flattened and anvil-shaped upper 1–3, slender and relatively elongate. There are 8–10 (mode 9), rarely 11, rakers on the lower part of this arch. No pseudorakers are developed (*see* p. 145).

Scales. Ctenoid; lateral line with 30 (f.6), 31 (f.13), 32 (f.14) or 33 (f.3) scales, cheek with 2 or 3 (mode) rows. Five to 6½ (mode 5½) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (mode), rarely 5, between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.1), 15 (f.28) or 16 (f.7) spinous and 8 (f.7), 9 (f.24) or 10 (f.5) branched rays. Caudal generally truncate but weakly emarginate in some fishes; scaled on its basal half. Pectorals 25·8–31·3 (M = 29·7) per cent of standard length, 79·5–94·5 (M = 87·3) per cent of head. Pelvics with the first ray slightly produced.

Teeth. The *outer teeth* in both jaws (except posteriorly in the upper) are slender, compressed and unequally bicuspid (text-fig. 7). The outline of the major cusp varies from equilateral to isoscelene; all intergrades may occur in one individual or one type of cusp outline may predominate. The crown is slightly incurved. Posterior teeth in the upper jaw are often either unicuspid and slender, or small, compressed and tricuspid. There are 40–60 (M = 52) teeth in the outer premaxillary row.

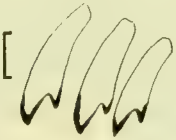

FIG. 7. *H. nigripinnis.* Premaxillary teeth (left), anterolateral in position. Viewed from an anterolateral position. Scale = 0·25 mm.

Teeth of the *inner rows* are small, compressed and tricuspid, and are arranged in 1 or 2 rows (rarely in 3) in the upper jaw, and 1 or 2 in the lower jaw. The serial arrangement of these teeth is often rather irregular.

OSTEOLOGY. The *neurocranium* of *H. nigripinnis* is identical with that of *H. elegans* and *H. aeneocolor*, that is, of a generalized type.

The *lower pharyngeal bone* gives an impression of being long, slender and fine (especially when compared with the bone in *H. elegans* or *H. aeneocolor*). Its dentigerous surface, however, is about 1·2 times broader than long. The teeth on this bone are fine, slender and cuspidate, and are arranged in *ca* 34 rows ; teeth situated on the posterolateral angles of the bone are more densely crowded than elsewhere.

Vertebral counts in the 13 specimens radiographed are 28 (f.1), 29 (f.9), 30 (f.2) or 31 (f.1), and comprise 12 (f.2), 13 (f.10) or 14 (f.1) abdominal and 16 (f.9) or 17 (f.4) caudal elements.

COLORATION IN LIFE. *Adult males* : ground colour (including that of the head) is a dark malachite green with a silvery underlay ; the branchiostegal membrane is black. On the head there is a prominent lachrymal stripe and a less intense interorbital bar ; both marks are intensified after death. The dorsal fin is dark grey, with black lappets, and a darker irregular line along the base ; a pink suffusion is visible over the soft part of the fin. The caudal has an overall pink flush except basally, where the membrane is dark hyaline. The anal is black over the spinous part, pinkish elsewhere (the colour intensifying distally) ; ocelli orange-yellow. Pelvic fins are black.

Adult females have an overall greyish-silver coloration above a midlateral line, and are chalky white below that level. The upper half of the caudal fin is hyaline but the basal area and lower half of the fin are suffused with pale lemon-yellow ; this pigmentation sometimes extends over the entire fin but even then is most intense on the lower half. Some individuals show dark rather elongate spots along the middle of the caudal. The anal has, distally, similar yellow colour to that of the caudal but it is hyaline basally. The dorsal and pelvic fins both are hyaline.

PRESERVED COLORATION. *Adult males* : the ground colour is dark brown to black below the midlateral line, and to varying degrees above that level as well. When dark pigment does extend dorsally it is generally less intense than on the ventral body. In some fishes up to seven dark, fairly narrow vertical bars extend across the light brown of the upper body ; sometimes there is a longitudinal dark bar extending for a variable length along the upper lateral line scale row.

The ventral half of the head is dark brown, the branchiostegal membrane black. A fairly distinct lachrymal stripe is usually visible through the general dark ground coloration of the snout. Two bars (of equal thickness) cross the snout, and often there is a small median blotch above the posterodorsal margin of the orbit. A larger dark blotch crosses the nape anterior to the dorsal fin origin ; this mark seems to be a medial continuation of the first vertical bar of the flank.

The dorsal fin is dark, black on its proximal half and dusky beyond ; the lappets are black. The caudal fin has a dark central area basally but otherwise it is greyish. The anal is black on its basal half, and dusky or hyaline distally. The pelvics are uniformly black or blotched black and dusky, the outer half of the fin being the darker part. The pectorals are hyaline.

Females have a greyish-silver to greyish-brown ground colour, and are lighter ventrally. In some few specimens very faint indications of vertical bars are visible on the flanks ; such marks are confined to the central flank region and do not extend as far as the dorsal or ventral body outline. All fins are hyaline, the dorsal sometimes greyish with dark lappets.

ECOLOGY. *Habitat.* Although predominantly a species of offshore areas and the open central part of the lake, *H. nigripinnis* is sometimes found within a few feet of the shoreline, especially where the substrate is sandy.

Food. As the long and coiled intestine suggests, *H. nigripinnis* is a vegetarian species. It feeds principally on suspended phytoplankton ; there is no indication from the gut contents of any bottom feeding habits. Like many *Haplochromis* species, *H. nigripinnis* is an opportunistic feeder ; insect remains (of both larvae and pupae) are recorded from the gut.

Breeding. Female mouth brooding is practised by *H. nigripinnis.* Of the 8 adult females examined, 5 have the right ovary noticeably larger than the left, 1 has the right ovary slightly the larger and 2 show equal ovarian development.

Distribution. Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Trewavas (1933) compared *H. nigripinnis* with *H. cinereus* (Blgr.) of Lake Victoria. The invalidity of this comparison has been commented upon above (p. 149). It is due entirely to there being, at that time, insufficient material of either species to permit of precise comparison.

Surprisingly, neither Trewavas (*op. cit.*) nor Regan (1921) compared *H. nigripinnis* with any other species in the Edward-George complex. *Haplochromis nigripinnis* is indeed a distinctive species, especially when its coloration, fine dentition, long gut, fine gill rakers and its feeding habits are considered. But, preserved specimens (or live females) have a great similarity with specimens of *H. macropsoides*, a new taxon described on p. 162.

Haplochromis nigripinnis differs from *H. macropsoides* in having finer outer teeth in both jaws, fewer rows of inner jaw teeth, a longer and more slender caudal peduncle, and in having a relatively larger opening to the nasal laterosensory canal (*see above*, p. 156).

The same character combination (and especially the dental ones) serves to distinguish *H. nigripinnis* from such species as *H. elegans*, *H. aeneocolor* and *H. limax.* In all instances, of course, male breeding coloration provides the most outstanding interspecific difference.

Outside Lakes Edward and George, the greatest morpho-anatomical (and ecological) resemblances are with *H. erythrocephalus* Greenwood & Gee, of Lake Victoria (Greenwood & Gee 1969). Both species have, besides a similar gross morphology, a diet of phytoplankton, fine and numerous teeth, slender gill rakers and a long, coiled intestine ; all, of course, correlated characters within each species. Male coloration is particularly different. Male *H. erythrocephalus* have a bright red head, while the head in *H. nigripinnis* is dark malachite green (*cf.* p. 157 above with p. 21 in Greenwood & Gee, *op. cit.*). There are several other interspecific differences, particularly in the pharyngeal dentition and the neurocranial shape. Skull form in *H. erythrocephalus* is more like that in the moderately specialized *Haplochromis* species, and the pharyngeal teeth are finer, more numerous and more densely arranged than in *H. nigripinnis*. *Haplochromis erythrocephalus* also has relatively longer and more slender gill rakers. In other words, *H. erythrocephalus* shows greater specialization for phytoplankton feeding than does *H. nigripinnis*.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 549–554	Tufmac Bay (trawl)
1972.6.2 : 598–601	Small island north of Kankurunga Island
1972.6.2 : 602–605	Small island north of Kankurunga Island
1972.6.2 : 606	Kashaka Bay
1972.6.2 : 607–611	Kashaka Bay
1972.6.2 : 648–654	East side of Akika Island
1972.6.2 : 636–647	Mid-lake *ca* 5 miles east of Kankurunga Island
1972.6.2 : 805 (figured specimen)	Small island north of Akika Island (trawl)

Haplochromis oregosoma sp. nov.

(Text-figs. 8 & 9)

HOLOTYPE. A female, 66·5 mm standard length, BMNH reg. no. 1972.6.2 : 141. The specific name (from the Greek *orego* to stretch and *soma* the body) alludes to the rather elongate form of this species.

DESCRIPTION. Based on 20 specimens, including the holotype, 48·0–72·5 mm standard length.

Depth of body 30·3–34·3 (M = 32·1) per cent of standard length, length of head 32·0–36·0 (M = 33·8) per cent. Dorsal head profile gently curved, less commonly straight, sloping at an angle of *ca* 35° to the horizontal ; dorsal margin of eye entering the profile or extending slightly above it.

Preorbital depth 10·5–15·2 (M = 13·3) per cent of head (showing ill-defined positive allometry with standard length), least interorbital width 20·0–25·0 (M = 22·3) per cent, ratio of interorbital width to eye diameter 1·5–1·8 (M = 1·7). Snout length 23·5–29·2 (M = 26·1) per cent of head, 0·7–0·9 (rarely 1·0) times broader than long ; eye diameter 33·4–41·2 (M = 38·2) per cent, depth of cheek 15·2–20·8 (M = 17·9) per cent.

Caudal peduncle 15·9–21·1 (M = 17·9) per cent of standard length, 1·4–2·0 (modal range 1·6–1·7) times as long as deep.

Mouth horizontal, lips not thickened. Length of upper jaw 28·6–34·7 (M = 31·7) per cent of head, length of lower jaw 38·1–45·6 (M = 41·9) per cent and 1·6–2·3 (mode 2·0) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye.

Intestine about $1\frac{1}{2}$ times the total length.

Gill rakers. The lower 1–3 on the first arch are reduced, the remainder either all slender and elongate or, less commonly, with the upper 2–4 flattened and branched. There are 9–11 (mode 10) rakers on the lower part of the first arch. No pseudorakers are developed.

Scales. Ctenoid ; lateral line with 30 (f.1), 31 (f.3), 32 (f.10) or 33 (f.5), cheek with 2 or 3 rows. Five to 6 (bimodal at $5\frac{1}{2}$ and 6) scales between the upper lateral line and dorsal fin origin, 5 or 6 (mode) between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.11) or 16 (f.9) spines, and 8 (f.5) 9 (f.9) or 10 (f.6) branched rays. Anal with 3 spines and 7 (f.1), 8 (f.8) or 9 (f.11) branched rays. Caudal slightly emarginate, scaled on its basal half or a little further posteriorly. Pectoral fin 25·6–30·0 (M = 28·1) per cent of standard length, 75·0–88·0 (M = 82·7) per cent of head. Pelvics with the first ray slightly produced.

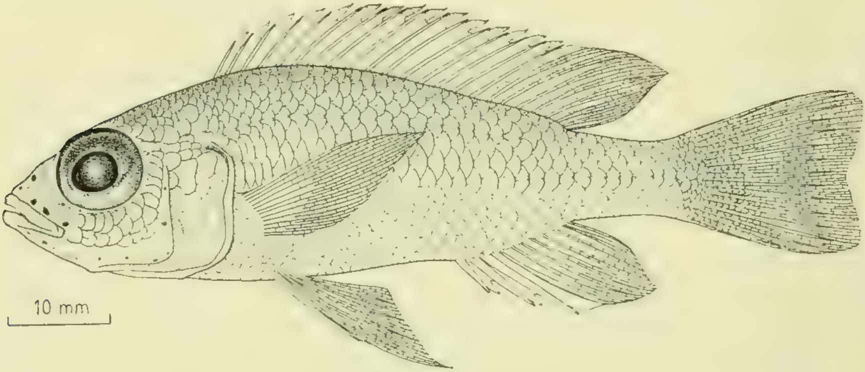

FIG. 8. *Haplochromis oregosoma.* Holotype.

Teeth. The predominant tooth form in the *outer row* of both jaws is a moderately slender, compressed and unequally bicuspid tooth (text-fig. 9). The major cusp in such teeth is produced, isoscelene in outline and slightly incurved. A distinct, step-like flange is sometimes developed on that margin of the cusp adjacent to the minor cusp. Some teeth may have the minor cusp greatly reduced in size. Posterolateral teeth in the upper jaw may be bicuspid like the others, slender unicuspids or compressed tricuspids. Tricuspid teeth are occasionally intercalated amongst the anteriorly situated bicuspids in either or both jaws. There are 42–60 (M = 50) outer teeth in the premaxilla.

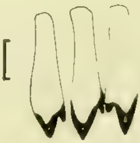

FIG. 9. *H. oregosoma.* Premaxillary teeth (left side), anterior in position. Viewed anteriorly. Scale = 0·25 mm.

Inner tooth rows in both jaws are composed of small tricuspid and compressed teeth, arranged in a single (rarely double) series.

OSTEOLOGY. Basically, the *neurocranium* of *H. oregosoma* is of the generalized *Haplochromis* type, but differs in having a low supraoccipital crest and a relatively shorter ethmo-vomerine region.

The *lower pharyngeal bone* is fine, its dentigerous area slightly broader than long (1·1–1·2 times). The teeth are slender and cuspidate, and are arranged in *ca* 26–30 rows.

Vertebral counts in the 12 specimens radiographed are 29 (f.3) or 30 (f.9), comprising 13 (f.5) or 14 (f.7) abdominal and 15 (f.1), 16 (f.8) or 17 (f.3) caudal centra.

COLORATION IN LIFE. *Adult males*: ground colour metallic purple above the midlateral line, shading through iridescent turquoise to silvery on the belly and ventral flanks; a sooty overlay spreads across the chest and belly. The dorsal fin is a dark sooty colour, as is most of the anal except for its scarlet tip; the anal ocelli are large, near circular in outline, and orange-yellow in colour. The entire caudal fin is scarlet, but the basal fifth may be sooty or solid black. The pelvic fins are uniformly black.

Adult females are an overall greyish-silver. The dorsal fin is hyaline, the anal pale yellow, the caudal dark hyaline and the pelvics greyish.

PRESERVED COLORATION. *Adult males*: ground coloration black or intensely dusky, with a silvery underlay; the chest and midventral aspects of the belly are light dusky. No distinct markings are visible on the head (probably they are obscured by the general dark coloration). Dorsal fin dusky to black, the pigment most intense between the rays. Anal black over its distal two-thirds, dusky beyond. Caudal with variable coloration but always dark over the proximal third; distally the fin is usually yellowish with a dusky overlay that intensifies between the middle rays. The pelvic fins are black, the pectorals hyaline.

Adult females are silvery-grey, shading to silver on the chest and belly; the dorsum and snout are dark grey. No cephalic markings are visible. All fins are greyish-hyaline.

BIOLOGY. Very little is known about the biology of *H. oregosoma*. Apparently the species is confined to offshore areas of the lake, and it does not occur close to papyrus or other shores. Specimens have been caught over both sand and mud substrata.

The breeding habits are unknown; of 9 adult females examined, 4 have the right ovary considerably larger than the left one, 4 have the ovaries equally developed and 1 has the left ovary larger than the right one. Individuals less than 55 mm standard length are immature, although males of 56 mm standard length are ripening. Fishes, of both sexes, are fully adult at 60 mm standard length.

Haplochromis oregosoma seems to feed on phytoplankton, but as yet too few specimens have been examined to establish whether the food is taken in suspension or from bottom deposits.

Distribution. Lake George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. From all other *Haplochromis* species in Lake George, *H. oregosoma* is distinguished by the following character combination: large eye, numerous and slender gill rakers, slender and elongate body form. Perhaps the species showing most superficial similarity with *H. oregosoma* is *H. nigripinnis*; the characters listed above, together with a difference in eye/interorbital ratio (1·5–1·8, mean 1·7, *cf.* 1·3–1·8, mean 1·5 for *H. nigripinnis*) serve to distinguish the species.

The totality of characters (including skull and jaw form) suggest that *H. nigripinnis* and *H. oregosoma* are probably not very closely related.

Among the Lake Edward species not recorded from Lake George, there is some resemblance between *H. oregosoma* and *H. engystoma* Trewavas. Unfortunately, *H. engystoma* is known only from the holotype (now in a poor state of preservation) and another, much smaller specimen which may not be a member of the species. Comparing *H. engystoma* holotype with *H. oregosoma*, the latter differs in having more gill rakers (10 or 11, *cf.* 8), straighter teeth, longer lower jaw (38·1–45·6, M = 41·9 per cent head, *cf.* 34·8 per cent in *H. engystoma*), and a slightly larger eye (33·4–41·2, M = 38·2 per cent head, *cf.* 34·8 per cent).

No known species from Lake Victoria shows any close resemblance to *H. oregosoma*.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 141 (Holotype)	North end of Kankurunga Island
1972.6.2 : 142–146 (Paratypes)	North end of Kankurunga Island
1972.6.2 : 147 (Paratype)	Northern tip Kankurunga Island
1972.6.2 : 148–152 (Paratypes)	Northern tip Kankurunga Island
1972.6.2 : 153 (Paratype)	Kankurunga Island
1972.6.2 : 154 (Paratype)	Tufmac Bay
1972.6.2 : 165 (Paratype)	In sandy shallows
1972.6.2 : 155–160	Tufmac Bay
1972.6.2 : 161–164	Tufmac Bay

Haplochromis macropsoides sp. nov.

(Text-figs. 10–12)

H. vicarius (part) Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 330–331 (1 of the paratypes, BMNH reg. no. 1933.2.23 : 353 from Worthington's station 613, Lake George. Trewavas incorrectly lists this station as '. . . East shore of Lake Edward ', but *vide* Worthington 1932).

HOLOTYPE. A male, 76·0 mm standard length, BMNH reg. no. 1972.6.2 : 718.

The trivial name refers to the overall similarity between this species and *H. macrops* (Blgr.) of Lake Victoria (and, so it was once thought, of Lake Edward as well).

DESCRIPTION. Based on 30 specimens (including the holotype, and the paratype of *H. vicarius, see above*), 59·0–77·0 mm standard length.

Depth of body 34·9–41·0 (M = 36·5) per cent of standard length, length of head 32·2–37·2 (M = 34·3) per cent. Dorsal head profile straight or very slightly curved, sloping at an angle of *ca* 35°–40° to the horizontal ; dorsal margin of the eye entering the line of the profile or extending slightly above it.

Preorbital depth 12·0–15·2 (M = 13·5) per cent of head, least interorbital width 20·5–25·0 (M = 23·1) per cent. Snout length 25·0–30·5 (M = 27·6) per cent, 0·8–0·9 times broader than long, eye diameter 33·3–39·1 (M = 36·0) per cent, showing very slight negative allometry with standard length, depth of cheek 17·5–23·8 (M = 21·4) per cent.

Caudal peduncle 13·6–19·3 (M = 15·8) per cent of standard length, 1·0–1·5 (modal range 1·2–1·3) times as long as deep.

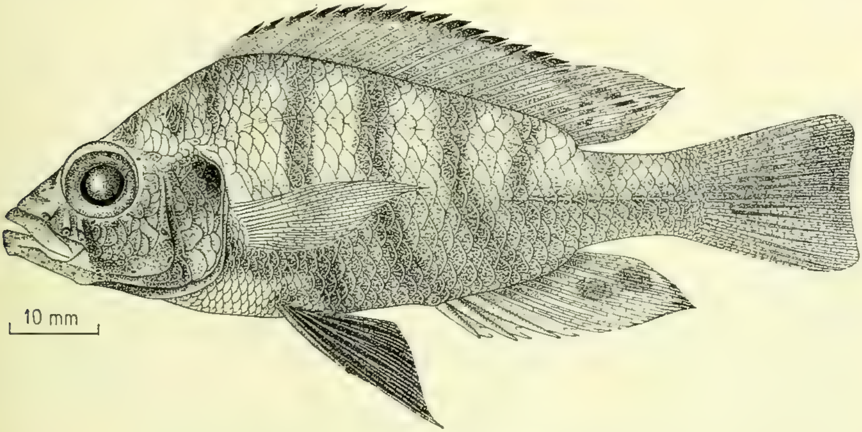

FIG. 10. *Haplochromis macropsoides*. Holotype.

Mouth horizontal, lips not thickened. Length of upper jaw 31·3–41·5 (M = 34·2) per cent of head, length of lower jaw 39·2–45·4 (M = 41·0) per cent, 1·7–2·2 (modal range 1·7–1·9) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye or somewhat behind that level.

The anterior opening to the nasal laterosensory canal is much smaller than the nostril (*cf. H. nigripinnis*), and indeed, can be difficult to locate.

The intestine is 1⅓–1½ times the total length.

Gill rakers. Except for the reduced lower 1 or 2 rakers, others on the first gill arch are relatively slender, although some of the uppermost ones may be flat and some lower ones stout. There are 8–10 (mode 9) rakers on the lower part of this arch. Pseudorakers are present, but are poorly developed and small.

Scales. Ctenoid; lateral line with 30 (f.2), 31 (f.9), 32 (f.15) or 33 (f.4) scales, cheek with 2 or 3 (bimodal) rows. Five to 6½ (mode 6) scales between the upper lateral line and the dorsal fin origin, 6 or 7 (rarely 5) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.4), 15 (f.20) or 16 (f.6) spinous and 8 (f.4), 9 (f.10) or 10 (f.16) branched rays. Anal with 3 spines and 8 (f.7), 9 (f.22) or 10 (f.1) branched rays. Caudal truncate or, less frequently, weakly emarginate; scaled on its basal half. Pectorals 25·7–32·3 (M = 29·4) per cent of standard length, 73·0–95·5 (M = 85·0) per cent of head. Pelvics with the first ray slightly produced.

Teeth. The majority of the *outer teeth* in both jaws are relatively stout, compressed and very unequally bicuspid; the larger cusp is isoscelene in outline and the crown slightly incurved (text-fig. 11). Posteriorly in the upper jaw the last few teeth are often slender and unicuspid. Some tricuspid teeth may be intercalated amongst the bicuspids anteriorly in either or both jaws.

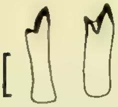

FIG. 11. *H. macropsoides.* Dentary teeth (right side), anterolateral in position. Viewed anteriorly. Scale = 0·5 mm.

As described for *H. elegans* (*see* p. 147), some bicuspids can have one margin of the major cusp produced into a narrow flange.

There are 42–60 (M = 52) teeth in the outer premaxillary series.

The *inner tooth rows* (2 or 3 in both jaws) are composed of tricuspid, compressed teeth.

OSTEOLOGY. The *neurocranium* of *H. macropsoides*, identical with that of *H. elegans*, *H. aeneocolor* and *H. nigripinnis*, is of a generalized *Haplochromis* type.

The *lower pharyngeal bone* (text-fig. 12) is moderately fine, with its dentigerous surface *ca* 1·2 times broader than long. The pharyngeal teeth are slender, compressed and cuspidate, and are arranged in *ca* 32–36 rows. Teeth in the two median rows are not noticeably coarser than their lateral congeners; teeth situated in the posterolateral corners of the bone are more closely set than elsewhere.

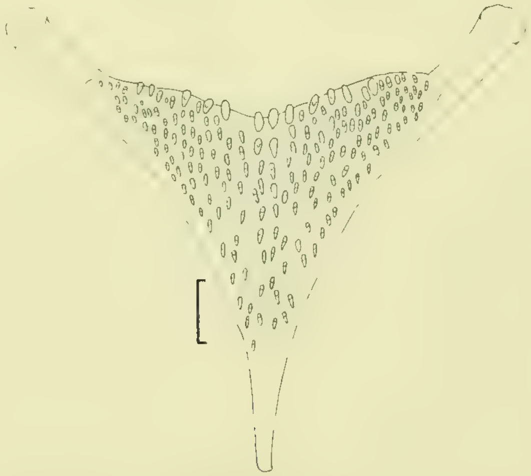

FIG. 12. *H. macropsoides.* Lower pharyngeal bone, occlusal view. Scale = 1·0 mm.

Vertebral counts in the 7 specimens examined are: 29 (f.6) or 30 (f.1), comprising 13 abdominal and 16 (f.6) or 17 (f.1) caudal centra.

COLORATION IN LIFE. *Adult males*: ground colour smokey grey overlying bluish-silver; snout, cheeks and lips a muted iridescent blue-green. Shortly after death, six faint vertical bars appear on the flanks; the first and second bars are separated by a greater distance than that between any of the succeeding bars. Dorsal fin with the spinous part sooty, the interspinous membrane generally darkest in colour; lappets black but with a narrow red streak or spot at the tip. Soft part of dorsal with maroon streaks between the rays. Caudal fin with maroon spots and blotches between the rays and a maroon flush around the margin. Anal dark hyaline (or faintly grey), dusky at the base but with a pinkish border. Pelvics are black.

In every major detail the adult, sexually active male coloration of *H. macropsoides* is identical with that of *H. elegans*. The sole colour difference, and that a subtle one, lies in the less brilliantly iridescent blue colour of the snout, cheeks and lips; in *H. macropsoides* the colour is more blue-green. More vertical stripes (9) appear after death in *H. elegans*.

I have been able to compare live fishes, of both species, in the same advanced state of sexual activity (i.e. ripe-running) and from the same locality. Except for the slight differences noted, I would consider the coloration to be identical. This is a most unusual situation amongst syntopic *Haplochromis* species and has not been recorded from the species flock of Lake Victoria. Further comment is reserved until p. 229.

Adult females have a golden-silver ground coloration shading to white on the belly. The dorsal fin has sooty lappets and an overall dark coloration except for reddish vertical stripes between the spines. The caudal fin is fairly dusky, with dark red streaks between the middle rays, and traces of red on the upper posterior margin. The anal is pale yellow, with a prominent orange spot occupying the position of an ocellus in a male fish. The pelvics are pale yellow.

PRESERVED COLORATION. *Adult males* have a generally dusky ground colour, darkest on the ventral aspects of the flanks and belly, but greyish-silver on the chest. At least 5 dark vertical bars are visible on the flanks; each bar extends from the dorsal to the ventral body outline. The head is dusky overall, with a distinct lachrymal stripe. Paired trans-snout bars are rarely visible, and then but faintly. No other cephalic markings can be detected (*cf. H. elegans*, p. 148). The branchiostegal membrane is black. The dorsal fin is dark grey to dusky, sometimes with a narrow black band along the entire base; the lappets are black, and the soft part of the fin is darkly maculate. Caudal fin greyish (darkest basally) and maculate but sometimes only weakly so. The anal is black or dark grey along its basal half, hyaline to light grey distally. The pelvics are dusky to black, the pectorals hyaline.

Adult females are greyish-silver, the ventral half of the body more silver than grey. No distinct cephalic markings are present. The dorsal and caudal fins are greyish hyaline, the margin of the dorsal often dusky. The caudal is immaculate, but has dark, ill-defined streaks between its rays. All other fins are hyaline.

ECOLOGY. *Habitat.* Not a great deal of information is available for this species, probably because in the field it is easily confused with *H. nigripinnis* and *H. elegans*. The specimens of *H. macropsoides* at my disposal are either from lake areas close to the fringing papyrus of islands (especially Kankurunga and Akika) or from more exposed areas offshore from these islands. In all localities the substrate is either sand with a thin mud overlay or organic mud.

Food. Only 6 of the specimens I have examined contained ingested material in the guts ; in all, this comprised dipteran larvae and pupae. As no other material was present (and particularly no phytoplankton or sand grains) the fishes may have been feeding away from the bottom.

Breeding. Haplochromis macropsoides is a female mouth brooder. All 7 of the adult, sexually active females examined have the right ovary much larger than the left one.

Distribution. Definitely recorded from Lake George and the Kazinga Channel (where it is scarce). The species probably occurs in Lake Edward as well since some specimens in the British Museum (Natural History), misidentified as *H. macrops* (Blgr.), a Lake Victoria endemic, are probably referable to *H. macropsoides.*

DIAGNOSIS AND AFFINITIES. As noted above (p. 165) the male reproductive coloration of *H. macropsoides* is virtually identical with that of *H. elegans.* However, the species clearly differ in a number of characters, including dentition (more outer teeth and more inner tooth rows in *H. macropsoides*) and the larger eye and longer upper and lower jaws of *H. macropsoides.*

From *H. nigripinnis, H. macropsoides* is distinguished by its deeper caudal peduncle (length/depth ratio 1·0–1·5, modal range 1·2–1·3, *cf.* 1·3–1·8, modal range 1·5–1·7 for *H. nigripinnis*), broader and more numerous inner tooth rows (3 in both jaws, *cf.* 1 or 2) and in having the anterior opening to the nasal laterosensory canal much smaller than the nostril (equal to it in *H. nigripinnis*). The species also differ in male coloration and, apparently, in their feeding habits (the intestine of *H. nigripinnis* is much longer and more coiled than that of *H. macropsoides,* and the former species is known to be a specialized phytoplankton eater).

From *H. oregosoma,* another large-eyed Lake George species, *H. macropsoides* differs in body form (depth 30·3–34·3, M = 32·1 per cent of standard length in *H. oregosoma, cf.* 34·9–41·0, M = 36·5 per cent ; also the caudal peduncle is more slender in *H. oregosoma,* namely 1·4–2·0, modal range 1·6–1·7 times longer than deep, *cf.* 1·0–1·5 modal range 1·2–1·3), in dentition (2–3 inner tooth rows in *H. macropsoides cf.* 1 in *H. oregosoma*), in neurocranial shape and in adult male coloration.

At first glance, *H. macropsoides* resembles *H. macrops* (Blgr.) of Lake Victoria. Closer inspection shows that the species differ in several characters. For example, the interorbital width is less in *H. macropsoides* (20·5–25·0, M = 23·1 per cent of head, *cf.* 26·6–32·2, M = 29·7 per cent in *H. macrops*), the eye is larger (33·3–39·1, M = 36·0 per cent of head, *cf.* 28·6–35·4, M = 33·0 per cent in *H. macrops*), the lower jaw is longer (39·2–45·4, M = 41·0 per cent head, *cf.* 38·0–42·5, M = 39·5) and the outer jaw teeth are fewer (42–60, M = 52, *cf.* 46–66, M = 60 in *H. macrops*). Male breeding coloration differs (*cf.* p. 164 above with p. 237 in Greenwood 1960). The supposed occurrence of *H. macrops* in Lakes Edward and George is discussed on p. 232.

Haplochromis velifer Trewavas of Lake Nabugabo resembles *H. macropsoides* in several respects. However, the species may be differentiated by the shallower preorbital of *H. macropsoides* (12·0–15·2, M = 13·5 per cent head, *cf.* 13·8–18·5, M = 16·3 per cent), the shorter snout (25·0–30·5, M = 27·6 per cent head, *cf.*

29·1–33·4, M = 31·3 per cent for *H. velifer*) and larger eye (33·3–39·1, M = 36·0 per cent head, *cf.* 26·3–33·4, *M* = 30·6 per cent); male coloration is also quite different in the two species (compare p. 164 above with pp. 321–322 in Greenwood, 1965b).

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 718 (Holotype)	Kankurunga Island
1972.6.2 : 723–728 (Paratypes)	Small island north of Kankurunga Island
1972.6.2 : 734–738 (Paratypes)	East side of Akika Island
1972.6.2 : 739–744 (Paratypes)	East side of Akika Island
1972.6.2 : 746–752 (Paratypes)	East side of Akika Island
1972.6.2 : 753 (Paratype)	Kankurunga Island
1972.6.2 : 754 (Paratype)	Kankurunga Island
1972.6.2 : 802–803 (Paratypes)	Kankurunga Island
1933.2.23 : 354 (Paratype)	Worthington collection
1972.6.2 : 719–722	Small island north of Kankurunga Island
1972.6.2 : 729–733	Small island north of Kankurunga Island
1972.6.2 : 755–756	Kankurunga Island
1972.6.2 : 757–765	East side of Akika Island
1972.6.2 : 766–772	Small island north of Kankurunga Island
1972.6.2 : 773–777	Small island north of Kankurunga Island
1972.6.2 : 778–783	Small island north of Kankurunga Island

Haplochromis limax Trewavas, 1933

(Text-figs. 13 & 14)

H. elegans (part) Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 332 (1 specimen, BMNH reg. no. 1933.2.23 : 395, collected by Worthington from Lake George [no other locality data given]).

? *H. nubilus* (part) : Trewavas, 1933, *op. cit.* (2 specimens BMNH reg. nos. 1933.2.23 : 301–302 from Lake George, are tentatively referred to *H. limax*).

HOLOTYPE. A male 80 mm standard length (BMNH reg. no. 1933.2.23 : 243) from Lake Edward.

DESCRIPTION. Based on 22 specimens (excluding the holotype), 61·0–84·0 mm standard length.

Depth of body 35·4–40·3 (M = 37·9) per cent of standard length, length of head 31·8–34·4 (M = 33·0) per cent. Dorsal head profile straight (rarely with a slight concavity or a slight convexity), sloping fairly steeply at an angle of *ca* 40°–45° with the horizontal.

Preorbital depth 13·6–18·2 (M = 15·4) per cent of head, least interorbital width 23·3–30·5 (M = 26·0) per cent. Snout 26·5–31·8 (M = 29·0) per cent, 0·8–0·9 (rarely 1·0) times broader than long; eye diameter 28·2–34·1 (M = 31·6) per cent, cheek depth 21·1–26·2 (M = 23·9) per cent. Caudal peduncle 13·6–18·1 (M = 15·3) per cent of standard length, 1·0–1·4 (mode 1·1) times as long as deep.

Mouth slightly oblique, lips a little thickened. Length of upper jaw 29·2–36·0 (M = 33·1) per cent of head (showing slight positive allometry with standard

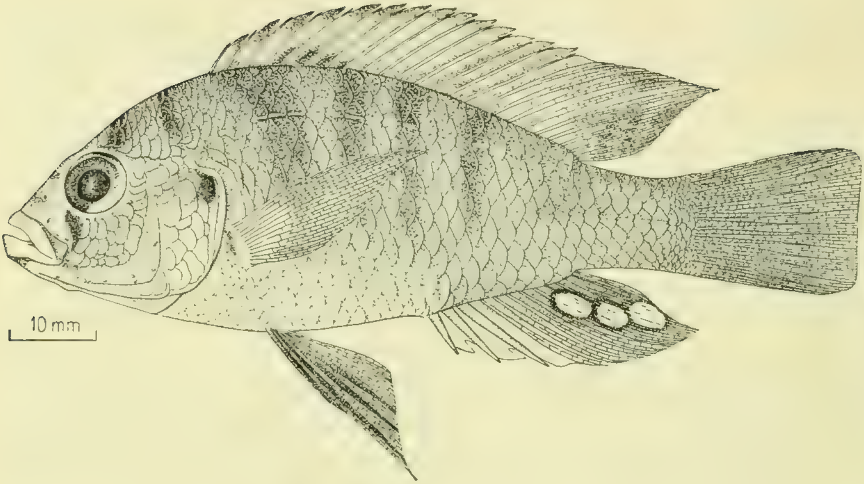

FIG. 13. *Haplochromis limax.* Lake George specimen ; a male.

length), length of lower jaw 36·0–40·9 (M = 38·3) per cent, 1·3–1·9 (modal range 1·4–1·6) times as long as broad. Posterior tip of maxilla reaching or almost reaching a vertical through the anterior margin of the eye.

Intestine long, *ca* 1½ to 1¾ times total length, and much coiled.

Gill rakers. Lower 1 or 2 rakers reduced, the remainder relatively slender or with 1 or 2 lower rakers short and stout. (One individual has no reduced rakers, but in this fish the total count is only 7 rakers.) There are 7 (rare) to 10 (mode 9) rakers on the lower part of the first gill arch.

The pseudorakers are well developed and are directed medially so that they overlie the true gill rakers of the inner row.

Scales. Ctenoid ; lateral line with 29 (f.1), 30 (f.9), 31 (f.8) or 32 (f.4) scales ; cheek with 2 or 3 (mode) rows. Five to 7 (rarely), mode 5½, scales between the upper lateral line and the dorsal fin origin, 5–6½ (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.4), 15 (f.15) or 16 (f.3) spinous and 8 (f.1), 9 (f.12) or 10 (f.9) branched rays. Anal with 3 spines and 8 (f.1), 9 (f.18) or 10 (f.3) rays. Caudal subtruncate, scaled on its basal half. Pelvics with the first ray produced. Pectoral 26·4–31·0 (M = 29·3) per cent of standard length, 80·0–98·0 (M = 89·1) per cent of head.

Teeth. Although basically the form of *outer row* jaw teeth is that of an obliquely cuspidate bicuspid, there is some individual variability, especially in the upper jaw (text-fig. 14). This variability concerns the angle of the cutting edge to the major cusp. In all specimens examined, this edge is most acute in teeth situated posterolaterally on the premaxilla ; teeth more anteriorly placed sometimes have the cusp so obliquely truncate that the cutting edge is almost horizontal. The modal condition, however, is one where the edge is at an angle of about 60° with the vertical. It may be noted that, in this respect, the Lake George fishes differ from the holotype whose teeth are of the more acute type.

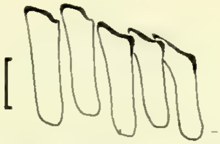

FIG. 14. *H. limax*. Dentary teeth (left), anterolateral in position. Viewed from a slightly ventrolateral position. Scale = 0·5 mm.

In the lower jaw, teeth tend to be more uniform with regard to cusp shape, and are like the modal upper jaw teeth already described. The minor cusp, in teeth of both jaws, is very small irrespective of major cusp shape. Posterior premaxillary teeth (usually the last 1–4 of the series) are generally unicuspid or are of the generalized bicuspid type, that is, with an acutely pointed major cusp.

There are 30–54 (M = 46) teeth in the outer premaxillary row.

Teeth of the *inner series* are invariably tricuspid and compressed. There are 4 or 5 (rarely 3) rows anteriorly in the premaxilla, and 3 or 4 (mode) anteriorly in the dentary ; laterally and posteriorly the number of rows, in both jaws, decreases to 1. A very distinct interspace separates the outermost row of the inner series from the outer row.

OSTEOLOGY. The *neurocranium* is of a generalized *Haplochromis* type but with the preorbital region more noticeably decurved than in *H. macropsoides* and *H. elegans*. Also, when compared with these fishes, the premaxilla of *H. limax* is more robust ; the dentary, however, is similar in all three species.

Comparison of *H. limax* syncranium with that in Lake Victoria species of similar feeding habits (i.e. scraping epilithic and epiphytic algae) shows that *H. limax* is more like *H. obliquidens* Hildg. and *H. lividus* Greenwood than *H. nigricans* (Blgr.). In the latter species the preorbital face of the skull is more strongly decurved and the dentary is deeper and more robust.

The lower *pharyngeal bone* in *H. limax* is moderately stout ; the dentigerous area is *ca* 1·2 times broader than long. The pharyngeal teeth are fine, compressed and cuspidate, and are arranged in *ca* 28–30 rows.

Vertebral counts in the 6 specimens radiographed are : 28 (f.5) and 29 (f.1), comprising 12 (f.1) or 13 (f.5) abdominal and 15 (f.4) or 16 (f.2) caudal elements.

COLORATION IN LIFE. *Adult males* : ground colour greyish, with a faint overlay of lime on the caudal peduncle and ventrally on the flanks as far forward as the anal fin. Laterally on the flanks and ventrally on the belly there is a scarlet flush, the intensity and area of which vary with sexual state. In quiescent fishes the flush is the colour of dried blood but it is bright scarlet in sexually active individuals. A similarly coloured flush is developed on the operculum and cheek.

The dorsal fin is dark hyaline with deep scarlet streaks between the spines ; between the branched rays the streaks are more precisely demarcated as scarlet lines. Anal fin is hyaline with a pink flush ; the ocelli are small and yolk-yellow in colour. The pelvic fins are dusky overall.

Adult females have a golden-grey ground colour, shading through silver to white on the lower flanks, belly and chest. The dorsal fin is hyaline but is somewhat dusky along its base. Caudal greyish-yellow, the yellow predominating basally. Anal fin also pale grey-yellow, with small, deep yellow spots in the position of ocelli in males. Pelvic and pectoral fins are hyaline.

PRESERVED COLORATION. *Adult males* : the ground coloration is silvery grey. The flanks and caudal peduncle are crossed by up to seven faint vertical bars, none of which extends ventrally below the level of the pectoral fin insertion. In some individuals a faint midlateral band is visible on the caudal peduncle, and extending forward to about a vertical through the origin of the soft dorsal fin. The chest, in some fishes, is sooty ; the branchiostegal membrane, in all, is black. A pair of parallel bars (of variable intensity) cross the snout ; a faint transverse bar extends across the head immediately behind the orbit, but in most specimens only that part of the bar immediately above the orbit is at all intense and discrete.

The dorsal fin is always dark, sometimes sooty, sometimes almost solid black between the rays ; the lappets are black. The caudal fin is greyish, becoming yellow on its ventral third ; in a few specimens there are concentrations of melanophores between the middle rays. The anal is greyish basally, yellowish distally. The pelvics are dusky to black on the outer (i.e. anterior) half, but yellowish elsewhere.

Adult females have a coloration similar to that of males, but the ground coloration is somewhat lighter and the pelvic fins are hyaline.

ECOLOGY. *Habitat.* The distribution of *H. limax* is closely correlated with the presence of emergent rooted vegetation, or of other places suitable for the growth of aufwuchs. *Haplochromis limax* has never been recorded far from the shore line, but the substrata over which it occurs are varied.

Food. Aufwuchs, its associated microfauna and macerated phanerogam tissue are the commonest types of ingested matter recorded from the gut. Little of the higher plant tissue is digested ; its occurrence in the gut is probably accidental and associated with the plant-scraping feeding habits of the species. Since sand grains and other inorganic bottom material are sometimes found in the gut, it is presumed that *H. limax* also feeds by scraping suitable food items from the lake bottom.

Breeding. Haplochromis limax is a female mouth brooder. Of the 6 adult females examined, 5 have the right ovary much larger than the left and 1 has the ovaries equally developed. One of the 2 smallest fishes available (both 61·0 mm standard length) is a juvenile, the other is a male with indications of early sexual development. At a standard length of 64 mm, fishes of both sexes are adult.

Distribution. Lakes Edward and George. The absence of this species from samples made in apparently suitable areas of the Kazinga Channel is noteworthy and inexplicable (*see* Appendix II).

DIAGNOSIS AND AFFINITIES. No other *Haplochromis* species in Lake George shows the dental characteristics of *H. limax* ; the male coloration is also highly diagnostic. In Lake Edward, on the other hand, there are two species, *H. serridens*

Regan and *H. fuscus* Regan, both with multiseriate inner tooth rows, and obliquely cuspidate outer teeth. *Haplochromis limax* is distinguished from *H. serridens* by its straighter dorsal head profile (distinctly curved in *H. serridens*), the fewer rows of inner teeth anteriorly in the jaws (3–5, *cf.* 5–8 in *H. serridens*) and by the presence of a distinct space between the outer tooth rows and the inner series of teeth. From *H. fuscus*, *H. limax* is distinguished primarily by the outer teeth having a broader and more obliquely truncate cusp, by the smaller size of the minor cusp on these teeth and by having a truncate (as opposed to rounded) caudal fin. In addition, preserved male *H. fuscus* are uniformly dark (nearly black) whereas *H. limax* males are silvery grey.

With so few specimens of *H. fuscus* and *H. serridens* available for comparison with *H. limax* it is impossible to evaluate the apparent interspecific differences in some morphometric characters. Data on live colours are not available for *H. serridens* or *H. fuscus*.

From the little information available, it seems reasonable to consider the three species closely related, with *H. serridens* the most specialized (at least in its oral dentition).

Trewavas (1933) noted similarities between *H. limax* and *H. vicarius*. Certainly the outer teeth in many of the *H. vicarius* specimens available do resemble the *H. limax* type. But, they are equally like those of *H. fuscus* (*see above*). It will be necessary to examine further samples of *H. vicarius*, and get information on live male coloration, before more definite conclusions can be reached on this possible interspecific relationship.

I have compared *H. limax* with those Lake Victoria species having a similar diet and dental specializations (viz. *H. lividus*, *H. nigricans* and *H. obliquidens*). All three species can be distinguished from *H. limax* by various characters or character combinations.

Tooth form and dental pattern in *H. limax* is most like that of *H. lividus*, but it is by no means identical. The teeth of *H. lividus* are more slender, their crowns are relatively less expanded, have curved not straight vertical margins, and are more movably implanted. On these characters, *H. lividus* would seem more specialized than *H. limax*.

The subequally, or almost subequally, bicuspid teeth of *H. nigricans*, coupled with the strongly decurved preorbital skull profile, and the relatively massive dentary of this species, all suggest that it belongs to a different lineage from that of the other Lake Victoria algal grazers. These same characters also serve to distinguish *H. nigricans* from *H. limax*.

The extreme modification of the teeth in *H. obliquidens* (*see* Greenwood 1956b) immediately distinguishes this species from *H. limax* but does not necessarily rule out a fairly close relationship between the species. The teeth in *H. obliquidens* seem to be the ultimate expression of a specialization already apparent in *H. lividus* and *H. limax* (*see* Greenwood, *op. cit.*, and above).

A fourth Lake Victoria species, *H. nuchisquamulatus* (Hildg.), has feeding habits similar to those discussed above. However, its teeth retain the basic, unequally bicuspid crown, and are not closely like those of *H. limax* (*see* Greenwood, *op. cit.*, and above).

Except for *H. nuchisquamulatus*, where it is not known, the breeding coloration of these species is clearly different.

Finally, comparison should be made with *H. annectidens* Trewavas of Lake Nabugabo. This species has about the same degree of resemblance to *H. limax* as does *H. lividus*. The same can probably be said of *H. astatodon* Regan of Lake Kivu, but far less is known about intraspecific morphological and dental variability in this species.

In brief, *H. lividus*, *H. limax*, *H. astatodon* and, despite its highly specialized teeth, *H. obliquidens* could well be members of a phyletic lineage.

STUDY MATERIAL

Registered number BMNH	*Locality*
1933.2.23 : 243 (Holotype)	Lake Edward (collected by Worthington)
1933.2.23 : 395	Lake George (collected by Worthington)
1972.6.2 : 112–118	Lake George, various localities
1972.6.2 : 119–123	Lake George, various localities
1972.6.2 : 124	Lake George, Akika Island
1972.6.2 : 125	Lake George, papyrus edge
1972.6.2 : 126–128	Lake George, Kankurunga Island
1972.6.2 : 129–135	Lake George, Kankurunga Island
1972.6.2 : 136–139	Lake George, Kankurunga Island
1972.6.2 : 140	Lake George, no locality
1972.6.2 : 808 (Figured specimen)	Lake George, Kankurunga Island

Haplochromis mylodon sp. nov.

(Text-figs. 15 & 16)

Haplochromis ishmaeli (*non* Boulenger) : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 334 (both specimens identified as *H. ishmaeli* are from Lake Edward).

HOLOTYPE. A male, 85·0 mm standard length, BMNH reg. no. 1972.6.2 : 656. The trivial name, from the Greek, refers to the mill-like crushing dentition of the pharyngeal bones.

DESCRIPTION. Based on 21 specimens (including the holotype), 68·0–115·0 mm standard length.

Depth of body 36·0–40·5 (M = 38·6) per cent of standard length, length of head 31·0–35·8 (M = 33·1) per cent. Dorsal head profile with some size correlated variation in outline, being more decurved in larger individuals and almost straight in smaller fishes ; sloping at an angle of 40°–45° with the horizontal at all sizes.

Preorbital depth 13·3–20·8 (M = 15·9) per cent of head, least interorbital width 24·1–28·6 (M = 26·6) per cent. Snout length 28·0–32·2 (M = 30·1) per cent of head, 0·8–0·9 (rarely 1·0) times its breadth, eye diameter 26·0–34·0 (M = 29·8) per cent, cheek depth 20·7–26·3 (M = 22·8) per cent. Caudal peduncle 14·7–18·4 (M = 17·9) per cent of standard length, 1·1–1·5 (mode 1·3) times as long as deep.

Mouth horizontal, lips not thickened. Length of lower jaw 35·2–40·5 (M = 37·6) per cent of head, 1·2–1·8 (modal range 1·5–1·6) times as long as broad. Posterior tip of premaxilla reaching a vertical through the anterior margin of the orbit or a little further posteriorly.

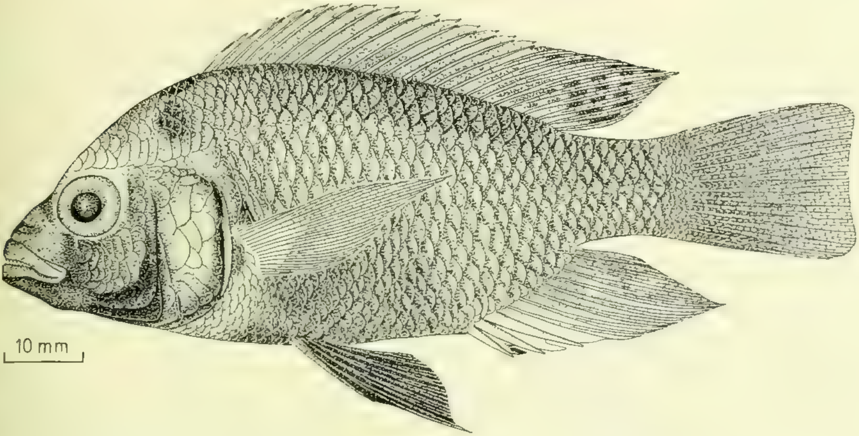

FIG. 15. *Haplochromis mylodon.* Holotype.

Gill rakers short and stout, the lower 1 or 2 reduced ; 7–9 (mode 7) rakers on the lower part of the first gill arch. The median row of pseudorakers on the first arch is well developed but individual pseudorakers are low.

Scales. Ctenoid ; lateral line with 31 (f.11), 32 (f.9) or 34 (f.1) scales, cheek with 3 (rarely 2) rows. Five to 7 (mode $5\frac{1}{2}$) scales between the upper lateral line and the dorsal fin origin, 6–8 (mode 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.2), 15 (f.10), 16 (f.8) or 17 (f.1) spinous and 8 (f.5), 9 (f.13) or 10 (f.3) branched rays. Caudal subtruncate, scaled on its basal half. Pectoral 27·6–33·3 (M = 29·5) per cent of standard length, 82·0–96·5 (M = 84·1) per cent of head. Pelvics with the first ray slightly produced.

Teeth. Except for 1 to 3 unicuspids posteriorly in the upper jaw of most fishes, the *outer teeth* in both jaws are stout and unequally bicuspid ; the major cusp is almost equilateral in outline, moderately protracted and barely incurved. There are 32–46 (M = 40) teeth in the outer premaxillary row.

The *inner* teeth are small and tricuspid, and are arranged in 1 or 2 rows in the upper jaw, and a single (rarely double) row in the lower one.

OSTEOLOGY. The neurocranium of *H. mylodon* is virtually identical with that of *H. ishmaeli* (or *H. pharyngomylus*) of Lake Victoria (*see* Greenwood 1960). The shape and size of the facet for the upper pharyngeal bones is strictly comparable in all three species, as is the relative contribution to this facet of the basioccipital and parasphenoid bones.

The *lower pharyngeal bone* is a massive structure (text-fig. 16). Compared with this bone in *H. ishmaeli* and *H. pharyngomylus*, that of *H. mylodon* is slightly less massive. The difference is not nearly so marked, however, as that between the bone in Lake Victoria and Lake George populations of *Astatoreochromis alluaudi* (*see* Greenwood 1959a, 1965b). The dentigerous area of the lower pharyngeal bone in *H. mylodon* is slightly smaller than in *H. ishmaeli* or H. *pharyngomylus*. Except in the outer rows, and in the posterolateral part of the toothed area, the lower pharyngeal teeth are all massive, stout and molariform (at least in the size range of specimens examined). Even the non-molariform teeth are stout, and are but weakly cuspidate. The extent of ' molarization ' in *H. mylodon* is thus comparable with that found in *H. ishmaeli* and *H. pharyngomylus*.

Vertebral counts in the 8 specimens radiographed are : 28 (f.1), 29 (f.6) or 30 (f.1), comprising 13 (f.8) abdominal and 15 (f.1), 16 (f.6) or 17 (f.1) caudal centra.

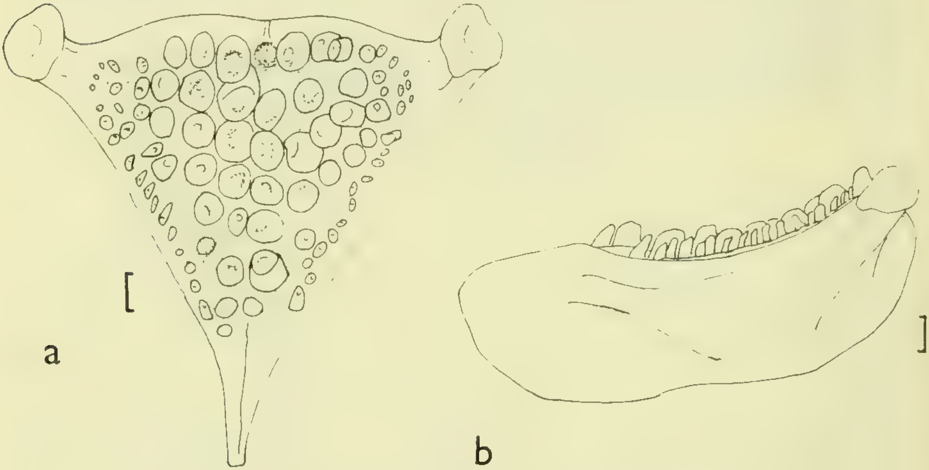

FIG. 16. *H. mylodon*. Lower pharyngeal bone. (a) In occlusal view. (b) In lateral view. From a specimen 110 mm standard length. Scale = 1·0 mm.

COLORATION IN LIFE. *Sexually active males* have a blue-grey ground colour with an iridescent turquoise sheen that is particularly concentrated around the margin of flank scales ; the belly is silvery grey, the chest and branchiostegal membrane are charcoal-grey. The head is blue-grey but the interorbital region is iridescent blue and is crossed by 2 dark bars. A prominent and dark lachrymal stripe continues to above the eye, where it expands to form a dark blotch. The dorsal fin is greyish-hyaline, the lappets are dusky, the soft dorsal has an orange-red to red margin, and there are dark red streaks between the rays. The caudal is dark over its proximal third, the remainder being rather dusky but with a red (crimson-lake) margin ; this red colour tends to extend forward onto the lower half of the fin, resulting in a dusky-pink coloration. The anal varies from dark hyaline to dusky pink on the spinous part (the lappets are black) ; the soft part is dark hyaline proximally, crimson to pink distally (the darker shades found nearest the middle of the fin). The anal ocelli are deep yellow. The pelvic fins are uniformly dusky.

In general, all colours are more intense in the sexually more active individuals.

Sexually quiescent and starting males have a light brassy ground colour with a pale-lime overlay, and are white on the chest and belly. The dorsal fin is dark hyaline, the soft part the darker. The caudal is yellowish basally, hyaline on the distal half, and has a bright orange-red margin that widens on the ventral half of the fin. The anal is pinkish, the pelvics dusky.

Adult females are silvery, shading to white on the belly. The dorsal fin is hyaline, as is the caudal which, however, has a yellowish flush on the ventral half and a bright scarlet posterior margin. The distal part of the ventral half of the caudal is also light scarlet. The anal fin is yellowish with a pinkish to scarlet overlay that is particularly intense along the margin of its soft part ; two orange spots occur in the position of the ocelli in males. The pelvic fins are hyaline or faintly yellow.

PRESERVED COLORATION. *Adult males* are brown above the midlateral line, shading to dark brown (almost bitter chocolate) below. Up to 8 rather narrow and fairly faint vertical bars are visible across the lighter part of the flank in some specimens ; ventrally the bars merge with the darker ventral flank coloration. The chest is dusky silver, the branchiostegal membrane dusky below the operculum but lighter between the jaws. The head, except for the operculum, is dark yellow-brown ; the operculum is even darker (i.e. it is comparable with the ventral flanks). There is a well-defined and broad lachrymal stripe, and two narrow transverse bars across the snout ; a broad, rather ill-defined band crosses the head behind the posterodorsal margin of the orbits, while another broad but more diffuse band or blotch extends across the nape immediately before the dorsal fin origin. The dorsal fin is dark grey, with short black blotches or streaks between the spines (at least basally). The soft part of this fin is darkly maculate. The caudal is greyish, becoming darker over its basal half. Proximally the anal is dark grey to dusky, the dark area becoming more extensive posteriorly and may occupy as much as the basal half of the fin. The rest of the fin is light yellowish-brown. The pelvics are dusky to black, the pectorals are hyaline.

Adult females are yellowish-brown to light greyish-brown dorsally, shading to silvery yellow on the belly and lower flanks. The dorsal and caudal fins are greyish, the anal, pelvics and pectorals are yellowish-hyaline.

ECOLOGY. *Habitat. Haplochromis mylodon* occurs near the shoreline over mud and mud–sand substrata. A few specimens have been caught in more open-water localities over a sandy bottom.

Food. Within the size range sampled, the diet of *H. mylodon* seems to consist mainly of gastropods, particularly *Melanoides tuberculata.* Chironomid larvae are also eaten.

Breeding. Haplochromis mylodon is a female mouth brooder. Individuals, of both sexes, less than 75 mm standard length are immature, and a few larger fishes (80 mm standard length) also show no signs of gonadial activity. Females may reach a larger size than the males ; the largest male recorded is 90 mm standard length, whereas the largest female is 115 mm standard length.

Distribution. Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Amongst the *Haplochromis* species of Lake George (and, apparently, also of Lake Edward), *H. mylodon* is immediately recognizable by its massive pharyngeal bones and dentition.

On the basis of purely anatomical characters, Trewavas (1933) very reasonably identified Lake Edward specimens of *H. mylodon* as *H. ishmaeli*, a species otherwise known only from Lake Victoria. Certainly on such characters it is difficult to distinguish between the two species. However, in life the coloration of adult, sexually mature males is very different (compare p. 174 above with p. 277 in Greenwood 1960).

When Lake George specimens are compared with *H. ishmaeli* from Lake Victoria (*see* Greenwood 1960) there are, in fact, some slight anatomical differences as well. For example, the cheek is a little shallower in *H. mylodon*, there are fewer teeth in the outer premaxillary tooth row than in *H. ishmaeli* and the chest scales are smaller.

A shallower cheek but larger chest scales and a longer pectoral fin distinguish *H. mylodon* from *H. pharyngomylus*, the other Lake Victoria species with a similar crushing pharyngeal dentition. Once again, adult male coloration provides a ready interspecific difference when live fishes are compared. But, in this instance the coloration is rather less different than in the case of *H. ishmaeli* and *H. mylodon*.

In brief, *H. mylodon*, *H. ishmaeli* and *H. pharyngomylus* are alike in nearly all morphometric characters and in most anatomical ones as well, but each species has a characteristic male coloration. It is chiefly because of the differences in coloration that I place *H. mylodon* in a distinct species (and do not include it with *H. pharyngomylus*). The importance of male coloration in cichlid courtship and species recognition is such that it would be biologically unsound to consider *H. mylodon* as anything other than specifically distinct.

Poll (1959) described three species (one from Lake Edward and two from nearby localities) with enlarged pharyngeal bones and molariform pharyngeal teeth. Of these species, one, *H. malacophagus* (from Lake Kibuga, *ca* 50 km south of Lake Edward), need not be considered in detail. Its pharyngeal bones and dentition are but slightly enlarged and there are other characters which differentiate it from *H. mylodon*.

The second species, *H. placodus* (from the Molindi River, near Lake Kibuga), has a greatly enlarged lower pharyngeal bone and an almost completely molariform pharyngeal dentition ; in both characters it is comparable with *H. mylodon*. In overall appearance, too, *H. placodus* is rather like *H. mylodon*. The holotype and only specimen (101 mm standard length) differs from *H. mylodon* in its larger pectoral and nuchal scales (4½ between upper lateral line and dorsal origin, 5 between pectoral and pelvic fin bases, *cf.* 5–7 [mode 5½] and 6–8 [mode 7] in *H. mylodon*), in having a much smaller eye (22·2 per cent of head, *cf.* 26–34·0, mean = 29·8 per cent) and a shorter pectoral fin (72·3 per cent head length, *cf.* 82·0–96·5, mean 84·1 per cent). When more specimens of *H. placodus* are available, its relationships with *H. mylodon* can be reviewed more critically. But, unless *H. placodus* holotype is an aberrant individual, it seems unlikely that the two species will prove to be conspecific.

The third species, *H. pharyngalis*, is from the western shore of Lake Edward, at Bugazia. In two of the three syntypes, the pharyngeal mill exhibits a degree of development almost comparable with that of *H. mylodon* and *H. placodus*. In the third specimen, however, the bones are not greatly enlarged and only the median rows of the lower pharyngeal teeth are molariform. Body form in *H. pharyngalis* is unlike that of *H. mylodon*, being elongate and slender. The thickened lips and slightly shorter lower jaw of *H. pharyngalis* give to the face a most distinctive appearance. Several other characters serve to distinguish this species from *H. mylodon* (and the other species considered here). Outstanding among these diagnostic features are the minute nuchal and chest scales. I count, in the three *H. pharyngalis* syntypes, 8 or 9 scales between the upper lateral line and the dorsal fin origin, and about the same number between the pelvic and pectoral fin bases ; furthermore, scales lower on the chest are so small and thin that, at first sight, this area seems naked. Other diagnostic characters are the low number of gill rakers (5 or 6), the longer snout (34·5 and 35·0 per cent head, *cf.* 28·0–32·2, mean 30·1 per cent in *H. mylodon*) and deeper cheek (26·7 and 29·3 per cent of head, *cf.* 20·7–26·3 per cent, mean = 22·8 per cent in *H. mylodon*). Because the two *H. pharyngalis* syntypes measured (82·5 and 88·0 mm standard length) are within the size range of the *H. mylodon* sample, these morphometric differences are unlikely to be the results of allometric growth. (The third syntype is rather distorted and was, therefore, not measured.)

There do not seem to be any grounds for assuming a close or even distant relationship between *H. pharyngalis* and *H. mylodon* (or, indeed, between that species and *H. placodus* or *H. malacophagus*). The peculiarly small nuchal and thoracic squamation of *H. pharyngalis* is, however, characteristic of a species recently discovered in Lake George (*see* p. 209). The two species also have a similar body form and physiognomy, but the new Lake George species does not have a hypertrophied pharyngeal mill ; their possible relationship is considered below (p. 213).

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 656 (Holotype)	Small island north of Kankurunga Island
1972.6.2 : 655 (Paratype)	N.E. corner of the lake
1972.6.2 : 657 (Paratype)	Over sandy shallows
1972.6.2 : 661–667 (Paratypes)	Various localities
1972.6.2 : 668–676 (Paratypes)	Various localities
1972.6.2 : 799–801 (Paratypes)	Small island north of Kankurunga Island
1972.6.2 : 658	Sandy shallows
1972.6.2 : 677–678	Locality unknown
1972.6.2 : 679–680	50–70 m from bush shore
1972.6.2 : 681	Locality unknown
1972.6.2 : 682	Locality unknown

Haplochromis angustifrons Blgr., 1914

(Text-figs. 17–19)

SYNONYMY. Trewavas (1933) gives a full synonymy for *H. angustifrons*, a species which Regan (1921) had previously synonymized with *H. schubotzi* Blgr.

Trewavas' redescription of the species (and her synonymy for it) was based entirely on Lake Edward specimens in the B.M.(N.H.) collections, which include 5 of Boulenger's syntypes (*see* Boulenger 1914 and 1915). One of the latter specimens was referred to *H. schubotzi* by Trewavas (*op. cit.*), and only 3 of the remaining 4 syntypes were included in her redescription of *H. angustifrons*. I have examined the fourth and neglected specimen, and can confirm its identity as *H. angustifrons*. The 4 syntypical specimens have the B.M.(N.H.) register numbers, 1914.4.8 : 25–28.

Through the courtesy of Dr K. Deckert (Berlin Museum) I was able to examine 48 syntypes of this species (including the specimen figured in Boulenger 1914 and 1915). It should be noted that there are apparently 53 syntypes in existence, although Boulenger (1914) originally recorded 56 specimens.

As far as I can tell without detailed knowledge of *H. angustifrons* in Lake Edward, all except 2 of the Berlin syntypes can be referred to this species. I do, however, have some reservations about the identity of a few small specimens in this series.

The 2 specimens which I do not consider to be *H. angustifrons* provide something of a puzzle that may only be solved when a large-scale revision of the Lake Edward *Haplochromis* species is carried out. Both these fishes are from the Berlin Museum lot number 19778. One, a female 71 mm standard length, appears to be of an *H. elegans*-like species. The other, a female, 86·0 mm standard length, I am tentatively referring to a new species described below (p. 188).

In his original description of *H. angustifrons*, Boulenger (1914) mentions some females as having '. . .einem breite, dunklen, braunen Seitenband vom kiemendeckel zur Schwanzflosse,. . .'. The 86 mm female mentioned above is the only syntype I examined with such a midlateral band. *Haplochromis angustifrons* females do not exhibit this colour pattern which is, however, a characteristic of the new species to which this syntypical fish is now tentatively referred (*see* p. 190 below).

As *lectotype* of *H. angustifrons* I have chosen the figured specimen, a male 91·0 mm standard length, Berlin Museum number 19118, collected by Schubotz from Lake Edward.

At least with respect to Lake George populations of *H. angustifrons*, the lectotype is unusual in being a male of such large size. In Lake George, adult males are generally much smaller than females. Despite this size discrepancy, the lectotype is a modal *H. angustifrons* in all morphological characters.

Trewavas' (1933) synonymy of *H. angustifrons* must now be expanded to include :

H. elegans (part) Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 333 (1 specimen from Lake George, BMNH reg. no. 1933.2.23 : 394).

H. vicarius (part) Trewavas, 1933, *op. cit.* : 331 (1 of the 2 paratypes from Lake George, [Worthington's (1932) station 613], BMNH reg. no. 1933.2.23 : 353).

H. schubotzi (part) : Trewavas, 1933, *op. cit.* : 337 (the 5 small specimens from Lake George, BMNH reg. nos. 1933.2.23 : 409–413, from Worthington's stations 613 and 627).

H. nubilus (part) : Trewavas, 1933, *op. cit.* : 329 (2 specimens, BMNH reg. nos. 1933.2.23 : 287 and 300, from Worthington's stations 613 and 618, Lake George).

H. guiarti (part) : Trewavas, 1933, *op. cit.* : 339 (1 specimen, BMNH reg. no. 1933.2.23 : 477, collected by Worthington from Lake George but no station number was given).

DESCRIPTION. Based on 41 specimens, 40·0–90·0 mm standard length, all from Lake George.

Depth of body 34·3–40·5 (M = 36·2) per cent of standard length, length of head 34·5–38·3 (M = 36·4) per cent. Dorsal head profile straight or very weakly convex, sloping at an angle of *ca* 35°–40° to the horizontal ; premaxillary pedicels prominent and breaking the dorsal head outline to give the fish a very characteristic ' Roman nose ' profile. The upper margin of the orbit just enters the line of the head profile.

Preorbital depth 12·5–18·9 (M = 16·6) per cent of head, least interorbital width 17·3–24·0 (M = 20·5) per cent, snout length 25·0–34·0 (M = 29·5) ; all three proportions show slight positive allometry with standard length. The snout varies from slightly broader than long to a little longer than broad (0·8–1·1), but modally is as long as broad.

The eye diameter and the cheek depth both show marked allometry with standard length, the former negatively allometric, the latter positively so. Thus, for these measurements two figures are given, first for fishes < 60 mm standard length (N = 12), and second for larger fishes (N = 29). Eye 32·3–37·6 (M = 35·1) per cent head, and 27·8–33·4 (M = 31·0) per cent ; cheek 15·3–23·7 (M = 21·3) per cent, and 22·7–29·6 (M = 25·7) per cent.

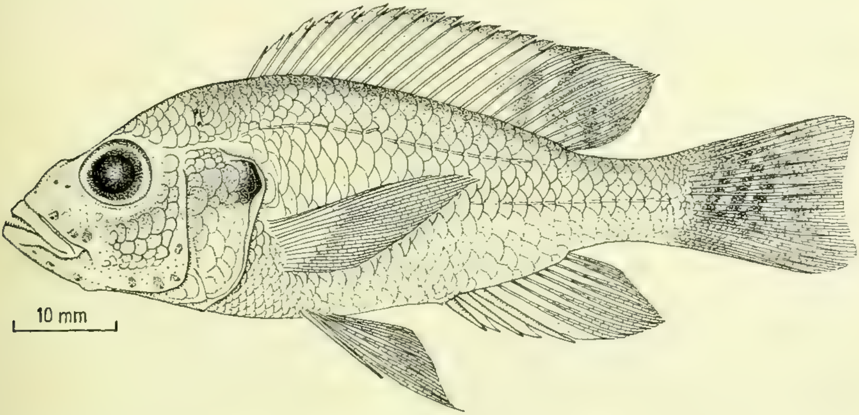

FIG. 17. *Haplochromis angustifrons.* Lake George specimen ; a female.

Caudal peduncle 15·6–20·0 (M = 17·5) per cent of standard length, 1·2–1·8 (modal range 1·3–1·5) times as long as deep.

Mouth slightly oblique, or horizontal ; lips not thickened. Length of upper jaw 30·2–37·5 (M = 34·4) per cent of head, length of lower jaw 38·8–45·8 (M = 42·5) per cent, 1·5–2·3 (modal range 2·0–2·2) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the eye or even through the pupil.

Gill rakers. The lower 1 or 2 rakers are reduced, the remainder relatively slender and elongate, although the rakers immediately above the reduced ones may be short and stout. There are 7 or 8 (rarely 10) rakers on the lower part of the first gill arch.

Pseudorakers are barely developed ; the tissue between the inner and outer rows of true rakers is slightly thickened and thrown into low and barely discrete projections.

Scales. Ctenoid; lateral line with 30 (f.13), 31 (f.22) or 32 (f.6) scales, the cheek with 2 (rare)–4 (mode 3) rows. Four and a half to 5½ (rarely 6½), mode 5, scales between the upper lateral line and the dorsal origin, 5–7 (rarely 8), mode 6, between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.15) or 15 (f.26) spinous and 8 (f.3), 9 (f.29) or 10 (f.9) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.29) or 9 (f.10) branched rays. Caudal truncate to very weakly emarginate, scaled on its basal half or a little further posteriorly. Pectoral 27·4–33·7 (M = 30·4) per cent of standard length, 74·0–89·9 (M = 83·1) per cent of head. Pelvics with the first and second rays somewhat produced.

Teeth. The *outer row* in the upper jaw usually is composed of both unicuspid and bicuspid teeth (text-fig. 18) the latter sometimes showing every gradation from fully and unequally bicuspid to weakly bicuspid (with the minor cusp virtually absent). As far as I can ascertain, this variability is not size correlated. All bicuspids, like the unicuspids, are slender and compressed; the major cusp is protracted, slightly incurved and has the outline of an isosceles triangle. Posteriorly in the upper jaw, the teeth are always unicuspid, and unicuspids generally predominate posterolaterally as well.

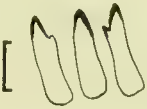

FIG. 18. *H. angustifrons.* Dentary teeth (left), anterolateral in position. Viewed laterally. Scale = 0·5 mm.

In general, the outer tooth row of the lower jaw has greater uniformity of tooth type. Unequally bicuspid teeth predominate.

There are 44–66 (mean 56) teeth in the outer row of the upper jaw, the number showing a slight positive correlation with size.

Tricuspid teeth predominate in the inner tooth series of both jaws, but many individuals have an admixture of tricuspid and weakly tricuspid teeth, or of unicuspids and weakly tricuspids. There are 1 or 2 (rarely 3) rows in both jaws.

OSTEOLOGY. The *neurocranium* closely resembles that in *H. schubotzi* and the new taxon, *H. schubotziellus* (*see* p. 190). It represents a somewhat specialized departure from the basic *Haplochromis* type; the preorbital region is relatively elongate and gently sloping, and there is an overall reduction in neurocranial width.

The *lower pharyngeal bone* is fine, its outline noticeably elongate and narrow (text-fig. 19), especially in comparison with the pharyngeal bone of other species in the Lake George flock. The dentigerous area is a little longer than broad (*ca* 1·1 times), the teeth fine, compressed and cuspidate and are arranged in *ca* 24–28 rows. Some teeth in the median rows are a little stouter than those situated laterally.

Vertebral counts for the 10 specimens radiographed are 28 (f.4) or 29 (f.6), comprising 12 (f.9) or 13 (f.1) abdominal and 16 (f.5) or 17 (f.5) caudal elements.

COLORATION IN LIFE. *Adult males*: the dorsum of the head and body is an iridescent violet which shades to turquoise on the midflank and greenish-golden on the belly. Chest and lower jaw are sooty, the branchiostegal membrane dusky to black, and the cheeks greenish-turquoise. Cephalic markings are not always visible, but when developed consist of a prominent, saddle-shaped nuchal bar and two parallel stripes across the snout.

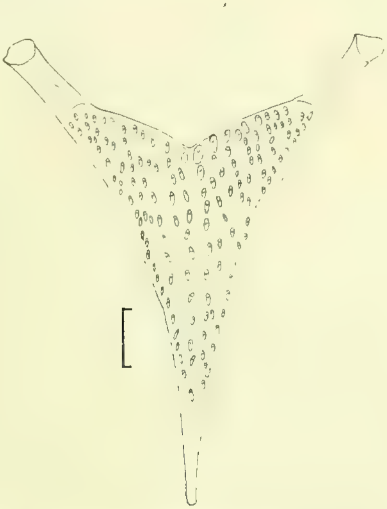

FIG. 19. *H. angustifrons*. Lower pharyngeal bone, in occlusal view. Scale = 1·0 mm.

The dorsal fin is dark hyaline with a sinuous black band running the entire length of the fin at a level about one-third of the distance between margin and base. Caudal fin dark hyaline, as is the anal which, however, is black basally and along its margin, and may show a faint pink flush; the anal ocelli are orange. The pelvic fins are black.

Shortly after death, traces of 7–10 vertical bars may appear on the flanks and caudal peduncle.

Adult females are metallic grey dorsally, shading through silver on the flanks to whitish on the belly. All fins are hyaline or faint yellow; the caudal is densely and clearly maculate, the spots dark grey and very obvious. (Indeed, this feature is diagnostic for the species in Lake George.)

PRESERVED COLORATION. *Males*: the ground colour is dark brown to black, the dark pigment most concentrated on the snout, cheeks, operculum, belly and lower half of the flanks. The lips are usually lighter than the cheeks, and the thoracic region is lighter than the flanks and belly. Traces of up to 6 narrow, fairly close-set vertical bars are often visible on the flanks. The bars are most distinct dorsally because ventrally they merge with the overall dark coloration for that region. Cephalic markings are not always visible, but when present consist of 2 bars across the snout, a lachrymal stripe, a large posteriorly directed triangular blotch on the posterior interorbital region, and a broad band across the nape.

The dorsal, pelvic and anal fins are dusky to black, the dorsal lappets intensely black ; the pigment on the dorsal and anal fins may be concentrated along the fin base. The caudal is lighter than the others, and has its pigment concentrated between the middle rays.

Females are silvery brown, some with faint traces of about 6 ill-defined vertical bars on the flanks. All fins are hyaline, but narrow dark streaks occur between the spines of the dorsal fin, and the soft part of that fin is sometimes weakly maculate. The caudal is invariably maculate, and distinctly so even if the spots are rather pale. (As in live fishes, this feature is a diagnostic one.)

ECOLOGY. *Habitat. Haplochromis angustifrons* is essentially an offshore species, and is rarely captured near any type of shore. In its habitat it occurs over both mud and sand substrates, but it seems to prefer the latter.

Food. Both planktonic and benthic animals are eaten, of which, respectively, chaoborid and chironomid larvae are the dominant food organisms.

Breeding. At least in the Lake George populations there is a very marked sexual dimorphism in the adult size attained. Males are noticeably smaller than females, individuals more than 65 mm standard length are rare, and the smallest male fish examined (40 mm standard length) was sexually active. Females, on the other hand, only reach sexual maturity at a length of about 63–65 mm, and attain a maximum adult size of at least 90 mm standard length. Some males do reach this size (one is known from Lake George, and the holotype, from Lake Edward, is 91 mm standard length) but are rare.

In addition to this sexually correlated size disparity, there also appears to be a marked imbalance in sex ratio at all times, but especially during daylight hours when males are particularly scarce (about 1 in 20 adult fishes). This problem of diurnal sex ratio change (with the concomitant problem of male ' migration '), and the apparently real predominance of females at all times and all places, is under active research by the I.B.P. team on Lake George. No further comments can be made at this time.

Of the 25 sexually active females sampled, 12 have the right ovary considerably larger than the left one, 6 have the left slightly larger and 7 have both ovaries equally developed.

Distribution. Lakes Edward and George, and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. *Haplochromis angustifrons* is immediately distinguishable from other Lake George *Haplochromis* species by its deep body, distinctive ' Roman nose ' profile and, at least in females, by the clearly maculate caudal fin. The distinctive coloration and small adult size of males are further diagnostic features.

Haplochromis angustifrons does not appear to be closely related to any other species in Lake George, nor, as far as can be estimated from known collections, to any species in Lake Edward. The dentition, narrow and elongate lower pharyngeal bone and the body form (especially head shape) distinguish this species from, on the one hand, the *H. elegans–macropsoides* complex, and on the other hand, from *H. schubotzi* and related species.

These same characters give *H. angustifrons* a superficial resemblance to *H. empodisma* Greenwood of Lake Victoria (*see* Greenwood 1960), and to *H. simpsoni* Greenwood of Lake Nabugabo (Greenwood 1965b). These two species are, however, distinguished from *H. angustifrons* by several morphometric and colour differences.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1933.2.23 : 287	Collected by Worthington, station no. 618
1972.6.2 : 412	Over sandy shallows
1972.6.2 : 414	Over sandy shallows
1972.6.2 : 420–428	Various localities
1972.6.2 : 432–433	Tufmac Bay
1972.6.2 : 434–437	Tufmac Bay
1972.6.2 : 438–440	Tufmac Bay
1972.6.2 : 441–500	Tufmac Bay
1972.6.2 : 512–515	Between Akika and Kankurunga Islands
1972.6.2 : 516–518	Kankurunga Island
1972.6.2 : 519–526	Small island north of Kankurunga Island
1972.6.2 : 531	Small island north of Kankurunga Island
1972.6.2 : 542–548	Small island north of Kankurunga Island
1972.6.2 : 804 (figured specimen)	Between Akika and Kankurunga Islands

Haplochromis schubotzi Blgr., 1914

(Text-figs. 20 & 21)

Haplochromis schubotzi (part) : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 337 (the 2 specimens 107 and 110 mm standard length, collected by Worthington. These specimens were not previously registered in the B.M. [N.H.] collection and are now given the reg. nos. 1972.2.24 : 1–2).

The five small specimens (52–80 mm standard length) from Lake George which Trewavas (*op. cit.*) mentions in her description of *H. schubotzi* are now identified as *H. angustifrons* (*see above*, p. 178).

The type series of *H. schubotzi* consists of 5 large males, all from Lake Edward (*see* Boulenger 1914). One of these fishes (reg. no. 1914.4.8 : 18) is in the collections of the British Museum (Nat. Hist.), the others are in the Berlin Museum. Through the courtesy of Dr K. Deckert I have been able to examine these specimens and thus to select a lectotype for the species.

LECTOTYPE. A male, 118·0 mm standard length, collected by Schubotz from Lake Edward (Berlin Museum number 19116). The three paralectotypes from that museum (also *ex* Lake Edward) have the lot number 22699.

DESCRIPTION. Based on 30 specimens from Lake George, 69·0–125·0 mm standard length.

Depth of body 33·7–39·3 (M = 36·4) per cent of standard length, length of head 32·5–37·8 (M = 34·9) per cent. Dorsal head profile straight or, less commonly, gently curved, sloping at an angle of *ca* 35°–40° with the horizontal.

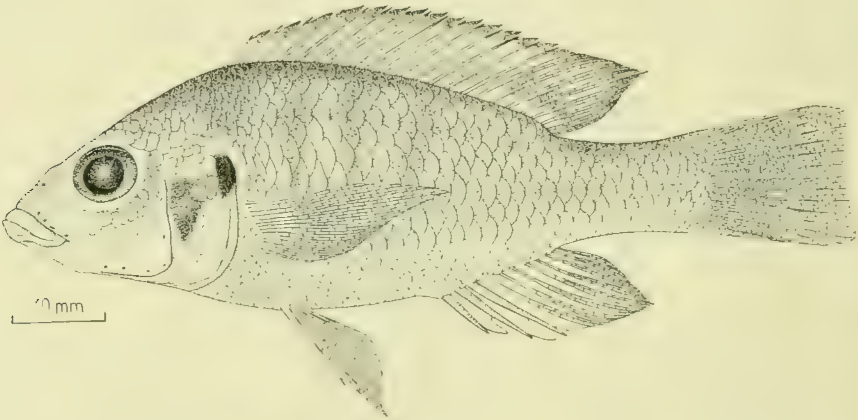

FIG. 20. *Haplochromis schubotzi.* Lake George specimen; a juvenile female.

Preorbital depth 16·4–20·9 (M = 19·0) per cent of head, least interorbital width 19·2–25·0 (M = 22·4) per cent; snout length 30·4–39·6 (M = 33·4) per cent, its breadth equal to (mode) or slightly greater than its length. Eye diameter 25·5–32·0 (M = 28·4) per cent of head, depth of cheek 20·7–26·0 (M = 22·8) per cent.

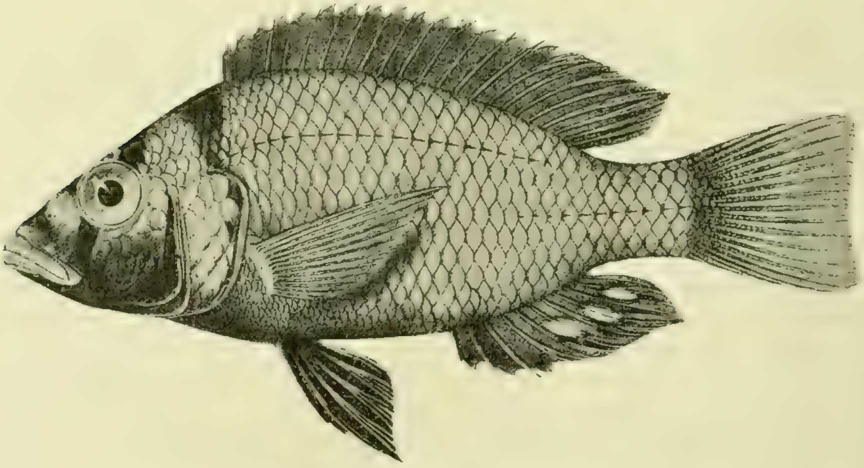

FIG. 21. *Haplochromis schubotzi.* A Lake Edward specimen (the lectotype). From Boulenger, *Cat. Afr. Fishes* (1915).

Caudal peduncle 16·2–19·2 (M = 17·7) per cent of standard length, 1·2–1·7 (modal range 1·3–1·5) times as long as deep.

Mouth horizontal, lips slightly thickened. Length of upper jaw 27·0–33·3 (M = 30·5) per cent of head, length of lower jaw 35·8–44·0 (M = 39·2) per cent, 1·4–2·0 (modal range 1·6–1·7) times as long as broad. Posterior tip of the maxilla usually reaching a vertical slightly anterior to the orbital margin, but reaching that level in a few fishes.

Gill rakers. A characteristic feature of the first gill arch in *H. schubotzi* is the well-developed papillose area of tissue immediately preceding the first (i.e. lowermost) gill raker. This raker, and usually the next one, is reduced ; the others are well developed and range in form from relatively stout to relatively slender. The pseudorakers on this arch are especially well developed.

There are 7 or 8 (mode) rarely 9 gill rakers on the lower part of the first arch.

Scales. Ctenoid ; lateral line with 31 (f.10), 32 (f.14), 33 (f.5) or 34 (f.1) scales ; cheek with 3 rows (rarely 2 or 4), the scales deeply embedded in the skin. Five to 6½ (mode 5½) scales between the upper lateral line and the dorsal fin origin ; 6 or 7 (deeply embedded) scales between the pectoral and pelvic fin bases.

Fins. Dorsal with 13 (f.1), 15 (f.17) or 16 (f.11) spinous and 8 (f.8), 9 (f.19) or 10 (f.2) branched rays ; anal with 3 spines and 8 (f.15) or 9 (f.15) branched rays. Caudal weakly emarginate, scaled on its basal half. Pectoral 25·6–30·0 (M = 27·6) per cent of standard length, 73·0–87·0 (M = 79·4) per cent of head. Pelvics with the first ray produced in adults, proportionately longer in males.

Teeth. Tooth form is loosely correlated with body size. In fishes less than 71 mm standard length, the *outer teeth* are clearly, but unequally bicuspid, the major cusp is produced and isoscelene in outline. In larger individuals the disparity in cusp size is more marked so that the inner cusp is virtually invisible ; the major cusp seems to be even more protracted and slender. At all sizes, the outer teeth are slender and compressed, with the crown slightly incurved. Irrespective of the fish's size the posterior and some posterolateral teeth in the upper jaw are relatively more slender than the others and are usually unicuspid or very weakly bicuspid. Elsewhere in this jaw (and particularly in larger fishes) there is usually an admixture of clearly bicuspid teeth, weakly bicuspids and, to a lesser extent, unicuspids.

Tooth form in the lower jaw is, on the whole, more uniform.

There are 46–62 (M = 52) teeth in the outer series of the premaxilla ; the number of teeth does not show any clear-cut correlation with standard length, but the two largest fishes (123 and 125 mm standard length) do have the two highest numbers of teeth recorded (60 and 62 for the fishes respectively).

The *inner series* in most fishes less than 90 mm standard length are composed of slender tricuspids, but in larger individuals there may be an admixture of tricuspids, weakly tricuspids and weakly bicuspids. All inner teeth are slender, and are generally implanted so as to lie horizontally. There are 3 rows (less frequently 2 or 4) in the upper jaw and 2 or 3 in the lower jaw.

OSTEOLOGY. The *neurocranium* of *H. schubotzi* shows many of the characters seen in the skull of *H. riponianus* (Blgr.) from Lake Victoria (*see* Greenwood 1960). In other words, it is a slightly specialized derivative of the generalized skull-type seen in, for example, *H. elegans*. The principal differences lie in the more elongate preorbital region of *H. schubotzi* skull, and in its straighter and less steeply sloping dorsal profile.

The *lower pharyngeal bone* is relatively slender, with its dentigerous area almost equilateral. The teeth are fine, compressed and cuspidate, and are arranged in from 26 to 30 rows. Some fishes have the teeth in the median rows slightly coarser than the others.

Vertebral counts in the 6 fishes radiographed are 29 (f.5) or 30 (f.1) comprising 12 (f.2) or 13 (f.4) abdominal and 16 (f.3) or 17 (f.3) caudal elements.

COLORATION IN LIFE. *Adult males* : the dorsum of the head, snout and body, the operculum and the anterolateral aspects of the flanks have a pinkish to orange-red flush ; the remainder of the body is blue-grey except for the sooty chest, and yellow tinge on the upper part of the caudal peduncle. Lips, lower margin of the preoperculum, the lower jaw and the lateral aspects of the snout are bright iridescent blue, or the cheek may be orange-red. Branchiostegal membrane is black but with traces of iridescent blue over its anterior half.

Dorsal fin dark but with reddish to orange streaks between the rays and a faint overall reddish-orange flush on the soft part ; the lappets are black. The caudal is hyaline with a faint red tinge between the rays, especially noticeable on the upper half of the fin. Anal bluish to dusky, the ocelli yolk-yellow. Pelvics dusky to black.

Immature males are basically silver-grey, with a faint rose flush on the operculum and anterior flanks, and some iridescent blue on the cheek and lips. Dorsal and anal fins are hyaline, the former with reddish streaks between the spines and rays ; caudal hyaline with a faint pink flush on its ventral half.

Adult females have a silvery-grey ground colour, shading to white on the belly. The dorsal, caudal and anal fins are hyaline with a faint yellowish to yellowish-grey flush, the pigment being most concentrated basally. The pelvic fins are hyaline.

PRESERVED COLORATION. *Adult males* : ground colour greyish-brown or greyish-silver above the midlateral line, becoming dusky silver ventrally. Lateral aspects of the belly and the entire thoracic region are dusky. The snout, cheeks and most of the opercular region are dusky or at least darker than the dorsum. Cephalic markings are of variable intensity depending on the basic tone of the head coloration. The lachrymal stripe is generally intense ; the snout is crossed by 2 bars, the upper of which is the wider and is often interrupted medially. On either side of the midline behind the level of the orbits is a dark, near-triangular blotch extending ventrally to the upper orbital margin ; an ill-defined black blotch crosses the nape, anterior to the dorsal fin origin.

The dorsal and anal fins are dark grey to greyish-brown, the margin of the soft part pale, the lappets of the dorsal black. The caudal is greyish, either darkest over its basal third or almost uniformly grey-brown. The pelvic fins are black or dusky, the pectorals hyaline.

Females are greyish to brown over a silvery underlay, silvery on the lower flanks and belly. Some individuals have very faint traces of transverse barring on the upper part of the body. Cephalic markings apparently are not developed save for a very faint lachrymal blotch. The dorsal and caudal fins are greyish, the soft dorsal sometimes maculate. The anal is hyaline to yellowish, the pelvics and pectorals are hyaline.

ECOLOGY. Virtually nothing is known about the feeding and breeding habits of *H. schubotzi*, and little is known of its distribution within Lake George.

Most of the specimens described above came from offshore localities, over sand or muddy sand substrates. Some localities are exposed, others relatively protected. Certainly the species is rarely caught in nets set close to a papyrus margin or close to other emergent aquatic plants; nevertheless it does sometimes occur in such habitats. Apparently the species is absent from the open waters of the centre lake.

The few available records of gut contents suggest that *H. schubotzi* is insectivorous, but the extent of its dependence on this food source requires confirmation.

It is still not known whether or not *H. schubotzi* is a mouth brooder. Fishes, of both sexes, less than 75 mm standard length are immature, as are some larger fishes (up to 80 mm standard length). Of the 8 adult females studied, 5 have the right ovary considerably larger than the left one and 3 have both ovaries equally developed.

Distribution. Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Probably the species from Lake George most like *H. schubotzi* is the new taxon *H. schubotziellus*. This species is described on p. 188, and its relationship with *H. schubotzi* is discussed on p. 192.

Superficially, *H. schubotzi* also resembles *H. mylodon* but is readily distinguished from that species by its unmodified pharyngeal bones, narrower interorbital (19·2–25·0, M = 22·4 per cent head, *cf.* 24·1–28·6, M = 26·6 per cent for *H. mylodon*), and by the presence of the extensive papillose area on the lower part of the first gill arch. In life, male breeding coloration is distinctive.

Rather less similar in its overall morphology is *H. angustifrons*, although small individuals of *H. schubotzi* could be confused with members of that species. *Haplochromis schubotzi* differs from *H. angustifrons* in having the inner jaw teeth horizontally aligned, in its shorter upper jaw (27·0–33·3, M = 30·5 per cent head, *cf.* 30·2–37·5, M = 34·4 per cent head), in possessing a papillose area preceding the first gill raker (*see above*), and in the failure of the posterior tip of the maxilla to reach the anterior orbital margin. Again, male coloration is diagnostic.

Considering species from outside Lakes Edward and George, *H. cinereus* (Blgr.) of Lake Victoria shares several characteristics with *H. schubotzi*. As pointed out before (Greenwood 1960), *H. cinereus* is, in fact, not the generalized species it was once thought to be by many workers. Its dentition and skull are relatively specialized when compared with the generalized *Haplochromis* type (Greenwood *op. cit.*). In these particular characters *H. cinereus* resembles *H. schubotzi*, as it also does in having well-developed pseudorakers and a papillose area before the lower gill raker (characters not previously recorded for *H. cinereus*). *Haplochromis cinereus* differs from *H. schubotzi* principally in having rather more unicuspid teeth in the jaws (at least when equal-sized fishes are compared) and in having the median teeth of the lower pharyngeal bone noticeably enlarged. The possible relationship of these two species will be considered again later in this paper (p. 233).

Gross morphology, neurocranial shape and dental characters are also similar in *H. schubotzi* and two other Lake Victoria species, *H. riponianus* (Blgr.) and *H. saxicola* Greenwood (*see* Greenwood 1960). The slender lower pharyngeal bone (lacking enlarged median teeth) of *H. schubotzi* is more like that of *H. saxicola* than that of *H. riponianus*. As usual, the coloration of adult males is different and there are morphometric characters distinguishing *H. schubotzi* from the two Lake Victoria species.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 683–685	Bay at the north end of Akika Island
1972.6.2 : 687–692	Bay at the north end of Akika Island
1972.6.2 : 697–698	Bay at the north end of Akika Island
1972.6.2 : 699	Bay at the north end of Akika Island
1972.6.2 : 700–701	Bay at the north end of Akika Island
1972.6.2 : 702–703	Off east shore of Akika Island
1972.6.2 : 704–705	Off papyrus edge of Akika Island
1972.6.2 : 706–707	Locality unknown
1972.6.2 : 708	Locality unknown
1972.6.2 : 709	1 m offshore from papyrus edge
1972.6.2 : 710	Over sandy shoal
1972.6.2 : 711–712	Locality unknown
1972.6.2 : 713	Northeast of Kankurunga Island
1972.6.2 : 714–715	Off Kankurunga Island
1972.6.2 : 716	Tufmac Bay
1972.6.2 : 717	Tufmac Bay
1972.6.2 : 807 (figured specimen)	Tufmac Bay

Haplochromis schubotziellus sp. nov.

(Text-figs. 22 & 23)

? *H. angustifrons* (part) Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped., 1907–1908, Zool.* **3** : 256–257 (1 of the paralectotypes in the Berlin Museum [no. 19778], a female 86 mm standard length from Lake Edward ; see also under synonymy of *H. angustifrons* on p. 178).

HOLOTYPE. A female, 76·0 mm standard length, BMNH reg. no. 1972.6.2 : 351. The trivial name (a diminutive) is given because, in the field, specimens of this species are often confused with small specimens of *H. schubotzi*.

DESCRIPTION. Based on 28 specimens (including the holotype) 45·0–79·0 mm standard length, all from Lake George. The syntype of *H. angustifrons* is not included because its identification as *H. schubotziellus* is tentative, and it comes from Lake Edward.

Depth of body 33·3–38·0 (M = 35·7) per cent of standard length, length of head 32·7–37·3 (M = 35·1) per cent. Dorsal head profile straight or gently curved, sloping at an angle of *ca* 35°–40° with the horizontal.

Preorbital depth 12·5–18·5 (M = 15·6) per cent of head, showing slight positive allometry with standard length; least interorbital width 17·9–20·8 (M = 19·5) per cent, length of snout 25·0–33·3 (M = 29·2) per cent, 0·8–0·9 times its breadth. Eye diameter 28·8–34·7 (M = 31·8) per cent of head, cheek depth 17·6–24·1 (M = 22·0) per cent, showing very slight positive allometry.

Caudal peduncle 13·3–18·5 (M = 16·5) per cent of standard length, 1·1–1·6 (modal range 1·3–1·4) times as long as deep.

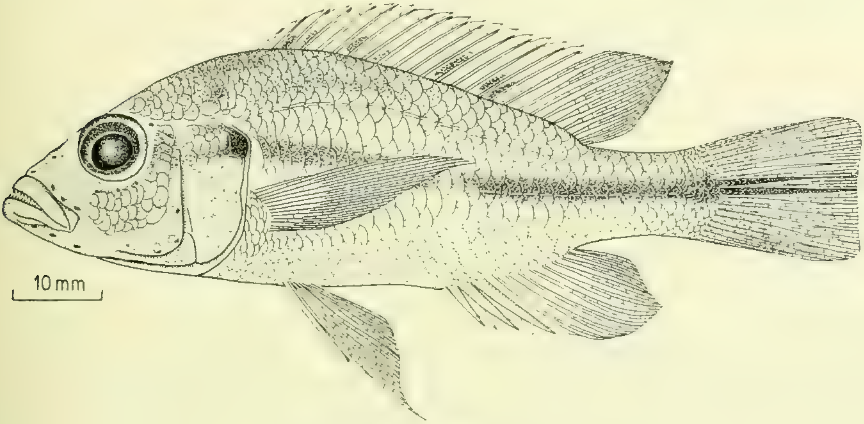

FIG. 22. *Haplochromis schubotziellus.* Holotype.

Mouth horizontal, lips very slightly thickened. Length of upper jaw, showing slight positive allometry with standard length, 28·2–37·0 (M = 34·2) per cent of head, length of lower jaw 36·7–45·0 (M = 41·6) per cent, 1·4–2·3 (modal range 1·7–1·9) times as long as broad. Posterior tip of the maxilla reaching a vertical through the anterior part of the orbit or a little further posteriorly.

Gill rakers. The tissue immediately anterior to the first gill arch is but slightly thickened, and is thrown into low, rather ill-defined folds (thus contrasting with *H. schubotzi* where this area is distinctly papillose and markedly pachydermatous). The first raker, and sometimes the 1 or 2 succeeding it, is reduced; the other rakers are short and relatively stout, with 7–9 (mode 8) on the lower part of the first arch. Pseudorakers are present but are small and sometimes ill defined.

Scales. Ctenoid; lateral line with 30 (f.1), 31 (f.9), 32 (f.15) or 33 (f.1) scales, cheek with 3 (rarely 2 or 4), rows, the scales not deeply embedded. Five to 6 (no distinct mode) scales between the upper lateral line and dorsal origin, 6 (mode) or 7, rarely 5 between the pectoral and pelvic fin bases, the scales not deeply embedded.

Fins. Dorsal with 14 (f.1), 15 (f.17) or 16 (f.10) spinous and 8 (f.1), 9 (f.18) or 10 (f.9) branched rays. Anal with 3 spines and 8 (f.17) or 9 (f.11) branched rays. Caudal weakly emarginate, scaled on its basal half. Pectoral fin 27·7–34·1 (M = 31·1) per cent of standard length, 78·0–94·5 (M = 88·9) per cent of head. First ray of pelvic fin produced, especially so in adult males.

Teeth. The predominant tooth type of the *outer row* in both jaws is a slender, very unequally bicuspid, with the major cusp produced, isoscelene to subequilateral in outline, and fairly strongly incurved (text-fig. 23). Slender unicuspids, and tricuspids, also occur in the outer row, and some fishes have all three types of teeth. A nearly constant feature is the presence of at least 1, usually 3, unicuspids at the posterior end of the premaxillary tooth row. Tooth form is less variable in larger fishes, where slender, strongly incurved unicuspids predominate.

There are 40–56 (M = 50) teeth in the outer premaxillary row.

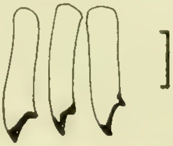

FIG. 23. *H. schubotziellus.* Premaxillary teeth (left), anterior in position. Viewed from anterior. Scale = 0·5 mm.

The *inner teeth* are tricuspid and broad, and are implanted so as to lie almost horizontally. Two (rarely 3) rows of inner teeth are found in both jaws.

OSTEOLOGY. The *neurocranium* of *H. schubotziellus* closely resembles that of *H. schubotzi*, but the dorsal preotic profile (especially anterior to the midpoint of the orbit) is somewhat more decurved in *H. schubotziellus.*

The *lower pharyngeal bone* is moderately stout and has an equilateral dentigerous area. The teeth are relatively fine, compressed and cuspidate, and are arranged in *ca* 20–24 rows. Teeth in the two median rows (especially those in the posterior third of the rows) are a little coarser than the others.

Vertebral counts in the 8 specimens radiographed are : 28 (f.2), 29 (f.4) or 30 (f.2), comprising 13 (f.5) or 14 (f.3) abdominal and 15 (f.3) or 16 (f.5) caudal centra.

COLORATION IN LIFE. *Adult males* : the ground coloration is greyish-silver with a faint iridescent blue-green sheen, particularly on the midflank region. The belly and ventral body surfaces are whitish. A fairly distinct, deep blue-black stripe extends midlaterally from the caudal fin base to the posterior opercular margin.

The dorsal fin is faintly sooty, with short black blotches along its base ; the lappets are black, the margin of the soft part is red and there are deep red spots between the branched rays. The caudal fin has similar red streaks on its proximal half and a pinkish-red flush distally. The anal is faintly dusky, with a slight pink flush ; the ocelli are orange-yellow. The pelvic fins are black.

Females are silver. A prominent black stripe runs midlaterally along the body and onto the caudal fin where it extends nearly to the midpoint. The band is of almost constant depth along the body but tapers somewhat on the fin. The dorsal fin, proximal half of the caudal and the distal part of the anal are hyaline with a suffusion of pale yellow.

PRESERVED COLORATION. *Adult males* : the ground colour is brownish above the midlateral line, greyish to sooty below ; the thoracic region is greyish to tarnished silver. The lower jaw is yellowish-brown, the branchiostegal membrane black.

Body markings are variable, but there is usually a complete dark midlateral band from the opercular margin to the caudal origin or else a band from about the middle of the body to the caudal base (sometimes this band is restricted to the posterior third of the body). Occasionally, a second longitudinal band is present, and follows approximately the course of the upper lateral line. Five to 7 rather faint but broad vertical bars are present on the flanks, and extend from the dorsal fin origin to about the level of the ventral margin of the pectoral fin. Cephalic markings are generally present (but faint) and comprise a lachrymal bar or blotch, a small blotch above and in contact with the posterodorsal margin of the orbit, and 2 faint, narrow bars across the nape.

The dorsal fin is greyish to dusky, the soft part generally maculate, the lappets dark or black. The caudal fin varies but usually is dark grey with lighter posterior and ventral margins ; otherwise the entire fin is light except for a central grey basal area. The anal is grey to dusky, particularly over the spinous part and along its distal margin. The pelvics are dusky to black, the pectorals hyaline.

Females have a light brown ground coloration shading to silver on the lower flanks and belly. A prominent and broad, dark midlateral band runs from the posterior opercular margin onto the basal part of the caudal fin ; in some specimens it extends to the posterior margin of the fin. This band is generally broken at about its mid-point, or at least is much thinner in that region. A second, but far less definite band runs a little above and parallel to the upper lateral line. The dorsal fin is greyish, often with dark lappets and sometimes with several concentrations of dark pigment along its base ; each blotch extends for a short distance upwards onto the fin membrane. The caudal fin is greyish (and has a continuation of the midlateral body stripe). All other fins are hyaline.

ECOLOGY. *Habitat.* The species is widely distributed in Lake George and occurs in most habitats. It is particularly common in muddy bays and near papyrus-fringed shorelines, but is rarely encountered in the open waters of the midlake region.

Food. Very little information is available on the food or feeding habits of *H. schubotziellus*. The presence in the gut of plant and other organic debris, together with dipteran larvae, suggests bottom feeding, possibly insectivorous habits.

Breeding. Almost no data are available on breeding habits. The size range of individuals available for analysis is such that one cannot tell precisely at what length sexual maturity is attained. The three smallest fishes examined (45–48 mm standard length) are immature ; the next smallest fish (66 mm standard length) and all others are adult and sexually active.

Of the 6 adult females studied, 4 have the right ovary much larger than the left and 2 have the gonads equally developed.

Distribution. Lake George and the Kazinga Channel (and probably Lake Edward as well).

DIAGNOSIS AND AFFINITIES. The close resemblance between *H. schubotziellus* and *H. schubotzi* has been noted already (p. 187). However, the species are immediately distinguishable on their coloration, even when preserved. The prominent midlateral band (especially in females) is diagnostic, and also serves to distinguish *H. schubotziellus* from all other species in Lake George (and probably Lake Edward as well). Compared with *H. schubotzi*, *H. schubotziellus* has a shallower preorbital (12·5–18·4, M = 15·6 per cent head, *cf.* 16·4–20·9, M = 19·0 per cent) a shorter snout (25·0–33·3, M = 29·2 per cent head, *cf.* 30·4–39·6, M = 33·4 per cent) a longer upper jaw (28·2–37·0, M = 34·2 per cent head, *cf.* 27·0–33·3, M = 30·5 per cent) and a longer pectoral fin (78·0–94·5, M = 88·9 per cent head, *cf.* 73·0–87·0, M = 79·4 per cent). There are also slight differences in the shape of the outer teeth, and in the relative stoutness of the lower pharyngeal bone (*H. schubotziellus* having a coarser bone with, usually, some teeth in the median rows noticeably coarser than the others).

This overall resemblance between the species means that *H. schubotziellus* also resembles the same Lake Victoria species as does *H. schubotzi* (*see above* p. 187). Indeed, the stouter lower pharyngeal bone and somewhat coarser median teeth in *H. schubotziellus* enhance its resemblance to *H. riponianus*, although in the latter species the lower pharyngeal dentition is rather more specialized (*see* Greenwood 1960). In many respects *H. schubotziellus* bears the same phenetic relationships to *H. schubotzi* as does *H. riponianus* to *H. saxicola* (Greenwood, *op. cit.*).

The relationship between *H. schubotzi* and *H. schubotziellus* could well be a truly phyletic one.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 351 (Holotype)	Kankurunga Island
1972.6.2 : 352 (Paratype)	Tufmac Bay
1972.6.2 : 353–355 (Paratypes)	Kankurunga Island
1972.6.2 : 356–358 (Paratypes)	Kankurunga Island
1972.6.2 : 359–366 (Paratypes)	Kankurunga Island
1972.6.2 : 367–372 (Paratypes)	Kankurunga Island
1972.6.2 : 373 (Paratype)	Kankurunga Island
1972.6.2 : 376–377 (Paratypes)	I.B.P. Jetty
1972.6.2 : 378 (Paratype)	I.B.P. Jetty
1972.6.2 : 374–375	Papyrus fringe of shore

Haplochromis taurinus Trewavas, 1933

(Text-figs. 24 & 25)

Haplochromis taurinus Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 336 (description based on Lake Edward fishes only).

HOLOTYPE. A female, 135·0 mm standard length, BMNH reg. no. 1933.2.23 : 406 from Lake Edward.

DESCRIPTION. Based on 12 specimens, 72·0–140·0 mm standard length, all from Lake George.

Depth of body 30·4–38·5 (M = 36·2) per cent of standard length, length of head 27·9–32·0 (M = 30·6) per cent. Dorsal head profile variable but usually concave, sloping at an angle of *ca* 40°–45° with the horizontal.

Preorbital depth 13·6–18·2 (M = 15·2) per cent of head, least interorbital width 22·2–29·6 (M = 25·4) per cent, length of snout 27·4–33·3 (M = 30·6) per cent, 0·7–0·9 of its breadth. Eye diameter 27·8–33·3 (M = 30·6) per cent of head, depth of cheek 23·7–30·0 (M = 27·1) per cent.

Caudal peduncle 15·7–19·0 (M = 17·0) per cent of standard length, 1·2–1·5 (modal range, 1·2–1·3) times as long as deep.

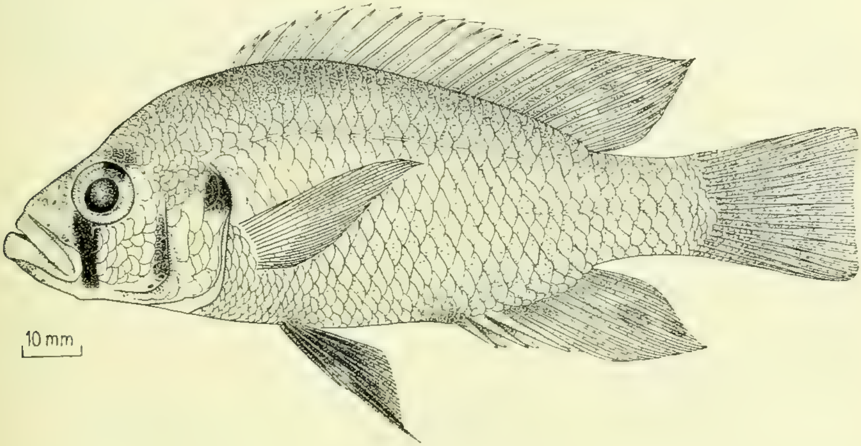

FIG. 24. *Haplochromis taurinus*. Lake George specimen ; an adult male.

Mouth somewhat oblique, lips thickened ; jaws equal anteriorly or the lower projecting a little. Upper jaw 38·0–42·3 (M = 41·0) per cent of head, lower jaw 43·3–56·0 (M = 46·8) per cent, 1·4–2·0 (modal range 1·6–1·8) times longer than broad. Posterior tip of the maxilla mostly exposed, reaching a vertical through the anterior part of the eye or one through the anterior margin of the pupil.

Gill rakers of variable form, from short and relatively stout to moderately long and slender ; the lower 1 or 2 rakers are reduced, the upper 2 or 3 often flattened and anvil-shaped. There are 8–11 (mode 9) rakers on the lower part of the first gill arch. No clearly defined pseudorakers are present on this arch, but the tissue between the inner and outer rows of gill rakers is raised into a distinct ridge with slight but circumscribed thickenings in the position usually occupied by pseudorakers.

Scales. Ctenoid ; lateral line with 31 (f.6) or 32 (f.6) scales, cheek with 3 (mode) or 4 rows. Five to 7 (mode 6) scales betewen the upper lateral line and the dorsal fin origin, 6 or 7 (rarely 8) between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.8) or 16 (f.4) spinous and 9 (f.7) or 10 (f.5) branched rays ; anal with 3 spines and 8 (f.4) or 9 (f.8) branched rays. Caudal subtruncate, scaled on its basal half or a little more. Pectoral fin 23·0–29·8 (M = 27·4) per cent of standard length, 81·5–100·0 (M = 89·3) per cent of head. Pelvics with the first ray noticeably prolonged.

Teeth. The *outer teeth* in *H. taurinus* show the form (text-fig. 25) which, in Lake Victoria *Haplochromis* species, is associated with paedophagus habits (Greenwood 1959b). Also, as in those species, the teeth of *H. taurinus* are deeply embedded in the mucosa of the jaws. In both jaws the basic tooth form is similar, namely a cylindrical neck and lower crown, but with a markedly compressed, chisel-like bicuspid upper crown. Upper jaw teeth have a crown in which the minor cusp is distinct and the major cusp is obliquely truncate ; the entire crown is curved inwards. Lower jaw teeth have the major cusp very obliquely truncate, the minor cusp distinct and the entire crown has a slight but definite outward inclination.

The posterior third to half of the premaxilla is edentulous ; the toothed part of the bone carries 32–48 (M = 36) teeth.

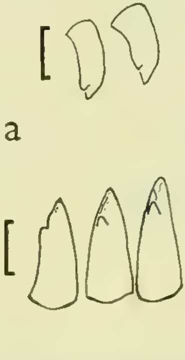

FIG. 25. *H. taurinus.* Teeth. (a) Premaxillary teeth (right), anterior in position. Viewed laterally. (b) Dentary teeth (right), anterolateral in position. Viewed from a point slightly anterior of lateral. Scale = 0·5 mm.

The *inner teeth* in both jaws are small and tricuspid, and are arranged in 1 or 2 rows. Like the outer teeth, those of the inner rows are deeply embedded in the mucosa.

OSTEOLOGY. The *neurocranium* of *H. taurinus* is of the generalized *Haplochromis* type. The premaxilla and dentary are also basically of a generalized type, the premaxilla not therefore showing the relative elongation of its ascending process (as occurs in some Lake Victoria paedophages, e.g. *H. parvidens*). Thus, in all syncranial features *H. taurinus* is comparable with the less specialized embryo and larval fish-eating species of Lake Victoria, viz. *H. maxillaris* and *H. obesus.*

The *lower pharyngeal bone* is relatively fine, its dentigerous area a little broader than long (*ca* 1·1 times). The teeth are slender, compressed and cuspidate, with those in the two median rows coarser than the others ; there are *ca* 20–22 rows of teeth.

Vertebral counts in the 7 specimens radiographed are 28 (f.1), 29 (f.5) or 30 (f.1), comprising 13 abdominal and 15 (f.1), 16 (f.5) or 17 (f.1) caudal centra.

COLORATION IN LIFE. *Males* : the live colours of sexually active males are unknown. A *juvenile male* had similar coloration to that of a female (*see below*) except that there were faint traces of a rosy flush on the operculum and anterior parts of the flanks (especially intense above the pectoral fin insertion). Other differences noted were that the lower limb of the preoperculum, the cheek and the lower lip were a pale iridescent blue. The dorsal fin had red streaks between the rays, as had the caudal fin where the colour was most intense on the middle of the fin. Two well-defined yolk-yellow ocelli were present on the otherwise hyaline anal fin.

Females, both adult and juvenile, have a silvery-grey ground colour shading to white on the belly, and a faint, yellowish overlay on the flanks (more intense in adults than in juveniles). The dorsal fin is hyaline but faintly yellow along its insertion. The caudal fin is yellowish-green over its basal half, pale yellow-green distally. The anal is faintly yellow, and the pelvics are hyaline.

PRESERVED COLORATION. *Adult males* are brownish above, shading to silvery grey (with faint dusky overtones) on the flanks and belly ; the chest is dusky silver, the branchiostegal membrane dusky grey. The head has a well-defined and intense lachrymal stripe continued through the eye and terminating as a blotch above and slightly behind the dorsal margin of the orbit. Other cephalic markings include a dark vertical arm of the preoperculum, and 2 rather faint transverse bars across the snout. A dark area just anterior to the dorsal fin origin is faintly visible. The dorsal fin is greyish, the caudal yellow-brown with traces of dark pigment between the rays (especially those in the middle of the fin). The anal fin is yellowish with a faint dusky overlay, the pelvics are black and the pectorals hyaline.

Females are light brownish-yellow above, shading to silvery yellow ventrally. The snout is grey-brown and there is an ill-defined and faint lachrymal stripe which does not extend through the eye to the dorsum. The dorsal and caudal fins are greyish (the former slightly the darker) ; all other fins are hyaline.

BIOLOGY. So few specimens of *H. taurinus* have been caught that it is impossible to generalize on the biology of the species. Apparently it is confined to inshore regions of the lake, where it has been taken off the papyrus fringe and also over sandy beaches in sheltered areas.

Judging from the dentition (*see above* p. 194) and the widely distensible mouth, *H. taurinus*, like similarly adapted species in Lake Victoria, feeds on the embryos and larvae of other cichlid fishes (*see* Greenwood 1959b). This supposition is borne out by the only two guts that yielded food remains. In these there were fragments of larval cichlids, bones of small fishes (of a size compatible with their being from larval fishes) and a fatty, yellow fluid closely resembling yolk.

Little information has been collected on the breeding habits of *H. taurinus*. The two available fishes less than 80 mm standard length are both immature ; all specimens of 83 mm standard length and longer are sexually active. Only 2 of the adult females examined have ovaries in an advanced stage of oogenesis ; in both fishes the right ovary is slightly larger than the left one.

Distribution. Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. Among the *Haplochromis* species of Lakes George and Edward, *H. taurinus* is immediately recognizable by its dentition (*see above* p. 194) and by its broad and laterally distensible mouth.

Outside these lakes, *H. taurinus* bears a close resemblance in both general morphology and in its dentition to *H. maxillaris* Trewavas of Lake Victoria (*see* Greenwood 1959b). Morphometric differences between the species are slight, with the jaws of *H. maxillaris* being somewhat larger and thus the gape in this species being a little greater than in *H. taurinus.* As far as can be told from the colours of juvenile male *H. taurinus* (compared with both adult and juvenile *H. maxillaris*) there is also a difference in this character. Taking all anatomical characters into consideration, *H. maxillaris* is the more specialized species of the two.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 29	Sandy shoal
1972.6.2 : 30	Kankurunga Island
1972.6.2 : 31–34	Papyrus fringe opposite I.B.P. Laboratory
1972.6.2 : 35	Locality unknown
1972.6.2 : 36–37	Locality unknown
1972.6.2 : 38–42	Locality unknown
1972.6.2 : 806 (figured specimen)	Kankurunga Island

Haplochromis labiatus Trewavas, 1933

(Text-figs. 26 & 27)

Haplochromis labiatus Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 335 (holotype and only specimen ; from Lake Edward).

Haplochromis labiatus was described from the holotype alone, although two smaller fishes were also mentioned (Trewavas 1933) ; all 3 specimens are from Lake Edward.

Only 1 specimen identifiable as *H. labiatus* has been caught in Lake George (from a locality close to the northern shore of Akika Island, in shallow water *ca* 1–1½ m deep, over mud, and near sparse stands of the reed *Phragmites*).

The Lake George fish is 87·0 mm standard length and is of indeterminable sex.

Depth of body 41·4 per cent of standard length, length of head 32·2 per cent. Dorsal head profile concave above the orbit, sloping steeply at *ca* 45° to the horizontal.

Preorbital depth 16·1 per cent of head, least interorbital width 24·3 per cent, length of snout 0·8 its breadth and 28·6 per cent of head length. Eye diameter 28·6 per cent of head, depth of cheek 25·0 per cent.

Caudal peduncle 14·1 per cent of standard length, 1·1 times its depth.

Mouth horizontal, lips noticeably thickened (but not produced into lobes medially) posterior tip of the maxilla reaching a vertical through the anterior part of the eye. Upper jaw 32·2 per cent of head, lower jaw 35·7 per cent, 1·4 times longer than broad.

Gill rakers. On the lower part of the first gill arch there are 8 rakers of which the lowermost is reduced, the following 2 are stout and the remaining 5 are relatively slender. Pseudorakers are present but weakly developed.

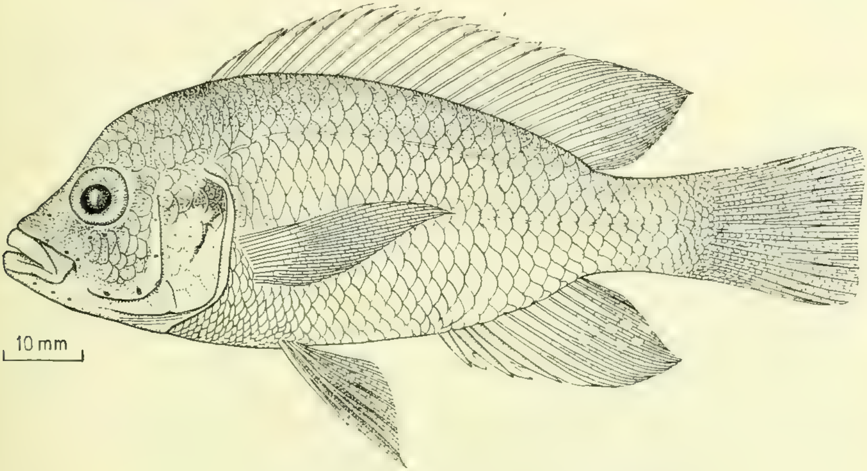

FIG. 26. *Haplochromis labiatus.* Lake George specimen.

Scales. Ctenoid, lateral line with 30 scales, cheek with 3 rows. There are $5\frac{1}{2}$ scales between the upper lateral line and the dorsal fin origin, 7 between the pectoral and the pelvic fin bases. Scales on the thoracic region are small.

Fins. Dorsal with 15 spines and 10 branched rays, anal with 3 spines and 9 branched rays. Pectoral 31·0 per cent of standard length, 96·5 per cent of the head. Caudal scaled on its basal half; the distal margin is frayed but was apparently truncate when intact. Pelvics with the first ray barely produced.

Teeth of the *outer row* in both jaws are stout and somewhat compressed (text-fig. 27). In the upper jaw the two posterior teeth on each side are unicuspid, but the remainder are unequally bicuspid, with the crown vertically orientated. There are 32 teeth in this row.

All teeth in the lower jaw are bicuspid, but those located posteriorly are smaller than the more anterior teeth. Anteriorly, the lower jaw teeth are slightly procumbent, each tooth lying forward at an angle of about 80° to the horizontal.

The *inner teeth* in both jaws are small and tricuspid, and are arranged in 3 rows in the upper jaw and 2 in the lower.

The *lower pharyngeal bone* is moderately stout and its dentigerous area is slightly broader than long (1·1 times). The teeth are compressed and cuspidate, with the posterior teeth of the median rows coarser than the others.

The *vertebral count* is 13 abdominal + 16 caudal centra. (The type has 13 + 17 centra.)

Only *preserved coloration* is known. The body is brownish above and shades to silvery on the ventral flanks, chest and belly; the entire head is brownish. All fins, except the pelvics, are hyaline-greyish, the soft dorsal is maculate posteriorly. The pelvics are dusky on the anterior half but hyaline posteriorly.

Distribution. Lakes Edward and George ; not yet recorded from the Kazinga Channel.

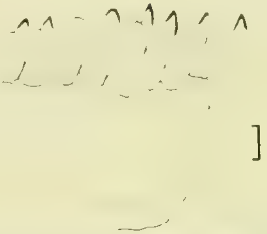

FIG. 27. *H. labiatus.* Dentary (anterior portion) with anterior and anterolateral teeth *in situ* (right side, viewed laterally) ; from the Lake George specimen. Scale = 0·5 mm.

COMPARISON WITH THE HOLOTYPE. The holotype is a larger fish (109 mm standard length) and is from Lake Edward. The Lake George specimen differs from the holotype in several minor ways, but in most details and in its overall morphology it resembles that specimen more closely than it does specimens of any other species.

The principal morphometric difference is in the longer jaws of the Lake George fish (35·7 and 32·2 per cent of head, *cf.* 32·3 and 28·0 per cent for the upper and lower jaws respectively) ; such a difference, however, is well within the range of variation for these characters in other *Haplochromis* species.

The lips of the holotype are clearly much better developed than are those of the Lake George specimen, and its teeth are predominantly unicuspid, not bicuspid as in the Lake George fish. However, some teeth in the holotype do show indications of a very small lateral cusp remnant. Both these differences could be attributable to the larger size of the holotype. Certainly the difference in lip development is well within the range of variation encountered in other species with hypertrophied lips and is not necessarily size-correlated. A further dental difference lies in the more clearly procumbent anterior teeth of the holotype. I am unable to comment on the sigficance of this character.

DIAGNOSIS AND AFFINITIES. As only two specimens are available (and those from different lakes) it is difficult to provide a precise diagnosis.

With so few specimens studied doubts might well be raised as to the validity of the species. However, if various dental and morphometric characters are combined, it seems most likely that *H. labiatus* is a valid species.

The teeth, thick lips and short lower jaw (*ca* 35 per cent of head) in *H. labiatus* together with its strongly concave profile distinguish the species from *H. limax* (teeth with obliquely cuspidate major cusps, compressed and relatively slender ; lower jaw 36·0–40·9, mean 38·5 per cent).

The concave profile of *H. labiatus* is an immediately obvious difference when a comparison is made with *H. elegans* ; the species also differ in that *H. elegans* has a shallower cheek (18·2–24·5, mean 20·8 per cent head, *cf.* 23·5 per cent), and has obviously bicuspid teeth, even in large specimens.

Dental differences like these noted above distinguish *H. labiatus* from *H. aeneocolor* (which also has more teeth in the premaxillary, viz. 40–56, mean 48, *cf.* 32), a longer lower jaw (38·0–44·0, mean 41·0 per cent head, *cf.* about 35·0 per cent) and a straight or convex dorsal head profile.

Similarly, the dentition and gross morphology serve to separate *H. labiatus* from other Lake George species. Within this lake the appearance of *H. labiatus* (and, basically, its dentition) is most like that of *H. elegans* and *H. aeneocolor*, but the resemblances are less close than are those with *H. beadlei* Trewavas of Lake Nabugabo, and with species of the *H. crassilabris* species complex in Lake Victoria. Unfortunately I have still to resolve satisfactorily the *H. crassilabris* problem (*see* Greenwood 1965b). Nevertheless, species of this complex can each be distinguished from *H. labiatus*. Characters separating *H. beadlei* from *H. labiatus* holotype were detailed in Greenwood (1965b). These will be found less trenchant when the Lake George fish is taken into account. More specimens of *H. labiatus* must be studied before the relationships, both phyletic and phenetic, of the two species can be settled.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 809	East side of Akika Island

Haplochromis pappenheimi (Blgr.), 1914

(Text-figs. 28–30)

Tilapia pappenheimi (part) Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped., 1907–1908, Zool.* **3** : 254–255 (10 of the 32 syntypes, all from Lake Edward, see note below).

T. pappenheimi (part) Boulenger, 1915, *Cat. Afr. Fishes*, **3** : 232–233 (4 of the 6 specimens listed, all from Lake Edward ; the figured specimen is not in the B.M. (N.H.) collections but is in Berlin [see below]. The skeleton listed cannot be identified with certainty, but probably it is not this species).

Haplochromis pappenheimi : Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 634–635 (all Lake Edward fishes).

Haplochromis pappenheimi : Trewavas, 1933, *J. Linn. Soc. (Zool.)*, **38** : 334 (all Lake Edward fishes).

NOTE ON THE TYPE SERIES. Six of the syntypes were deposited in the British Museum (Natural History) ; the other 26 specimens were retained by the Berlin Museum.

Regan (1921) reviewed the B.M. (N.H.) material and referred 2 specimens to the new species *H. nigripinnis* and *H. eduardii* described in that paper. Regan did not examine the Berlin syntypes, and no lectotype was chosen. The 4 remaining syntypes were considered conspecific by Regan, a conclusion with which I concur.

Through the kindness and cooperation of Dr Deckert, I have been able to study the 26 syntypes (including the figured specimen) from the Berlin Museum collections. This series proved to be polyspecific and cannot be fully evaluated until the Lake Edward *Haplochromis* species are revised. For the moment, however, it should be noted that 12 syntypical specimens are conspecific and are considered to be *H.*

pappenheimi (*see below*). The other specimens, in part, are probably referable to *H. nigripinnis* (8 specimens Z.M. Berlin, nos. 22693 and 22698), *H. eduardii* (2 specimens, Z.M. Berlin, no. 22692) and 2 specimens to species as yet undescribed (Z.M., nos. 22695 and 22696).

Boulenger's (1914) original description of *H. pappenheimi* is quite inadequate by current standards, and thus it is impossible to determine from it the morphological limits of his species. The reason for my deciding that certain specimens are '*H. pappenheimi*' is essentially an attempt to avoid unnecessary nomenclatural change. There is certainly a biologically and morphologically valid taxon, occurring in both Lakes Edward and George, whose characteristics are recognizable in 16 of the *H. pappenheimi* syntypes (4 specimens from the B.M. [N.H.] and 12 from the Berlin Museum (Z.M.B. lot nos. 22689 and 22697). The four B.M. [N.H.] fishes are those on which Regan [1921] based his redescription of the species).

It is to these 16 specimens that I have decided the name '*pappenheimi*' should be restricted and from which the lectotype should be chosen. If any of the other syntypes was chosen as lectotype, then the name '*pappenheimi*' would either fall into synonymy or would replace the name of an already established taxon. Either way, a new name would have to be found for the taxon here considered to be *Haplochromis pappenheimi*.

Regrettably, the specimen illustrated in Boulenger (1914, 1915) cannot be referred to the taxon *H. pappenheimi* as recognized by Regan (*op. cit.*) or myself. It is a fish of 66·0 mm standard length, probably a female, ZMB no. 22692. As far as I can determine this fish is a specimen of *H. eduardii* Regan.

To avoid the nomenclatural changes that would follow the choice of this fish as lectotype, I have selected for that purpose a specimen from the 16 syntypes showing the diagnostic features of *H. pappenheimi*, *sensu* Regan (1921). This fish, a female 73·0 mm standard length (ZMB no. 19110) has a characteristically elongate and slender body, and also clearly shows the dental and gill raker characters of the species (text-fig. 28).

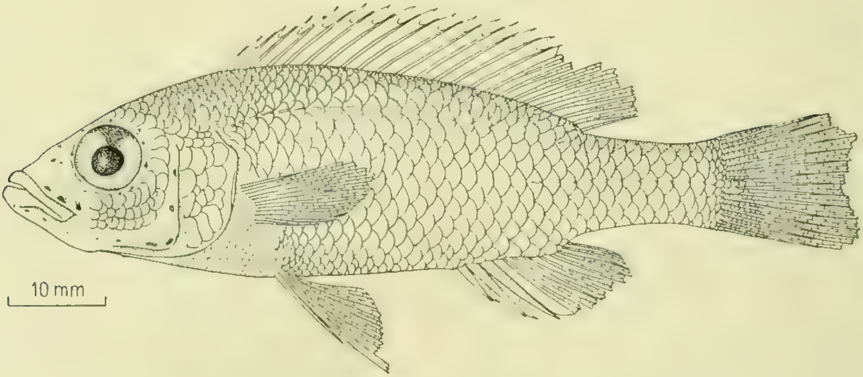

Fig. 28. *Haplochromis pappenheimi*. Lectotype; a Lake Edward specimen.

DESCRIPTION. Based on 20 specimens, 38·5–61·0 mm standard length, all from Lake George.

Depth of body 26·6–30·4 (M = 29·9) per cent of standard length, length of head 30·5–34·4 (M = 32·3) per cent.

Dorsal head profile straight, sloping gently at an angle of *ca* 20°–25° with the horizontal.

Preorbital depth 12·5–16·8 (M = 14·8) per cent of head, least interorbital width 23·3–29·2 (M = 26·4) per cent, length of snout 1·0–1·1 times its breadth, and 24·0–30·8 (M = 28·1) per cent of head. Eye diameter 31·5–37·0 (M = 33·9) per cent (not showing any allometry in this size range), depth of cheek 13·4–19·5 (M = 17·0) per cent.

Caudal peduncle 19·5–24·5 (M = 22·2) per cent of standard length, 1·5–2·0 (modal range 1·7–1·8) times as long as deep.

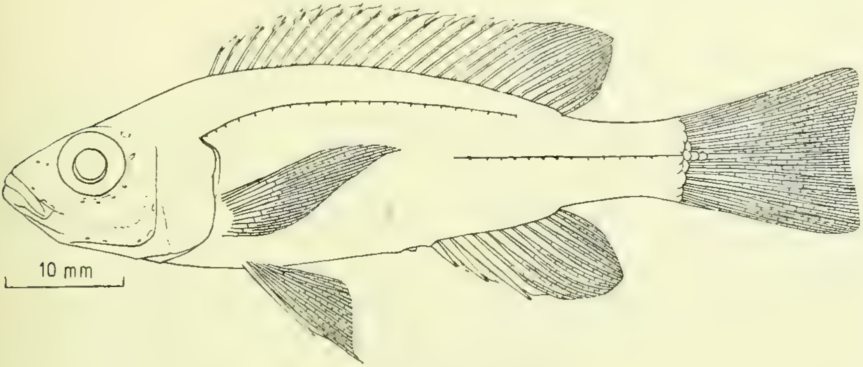

FIG. 29. *H. pappenheimi.* Outline drawing of a Lake George fish.

Mouth slightly oblique, jaws equal anteriorly. Posterior tip of the maxilla reaching a vertical slightly anterior to the orbital margin. Upper jaw 25·0–29·2 (M = 27·5) per cent of head, lower jaw 35·7–41·5 (M = 39·0) per cent, 1·7–2·5 (modal range 2·3–2·5) times longer than broad.

Gill rakers. The lower 1 or 2 rakers (rarely the first 4) are reduced, the others are long and relatively slender. Occasionally some of the uppermost rakers are flattened, or flattened and bifid. There are 10(rare)–13, mode 11, rakers on the lower part of the first gill arch. No pseudorakers are present.

Scales. Ctenoid ; lateral line with 33 (f.7) or 34 (f.12) scales, cheek with 2 or 3 rows. Five (rarely) to 7 (mode 6) scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.1), 15 (f.10) or 16 (f.9) spinous and 8 (f.4), 9 (f.11) or 10 (f.5) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.7) or 9 (f.11) branched rays. Caudal slightly emarginate, scaled on its basal half or slightly more. Pectoral fin 22·0–27·5 (M = 25·0) per cent of standard length, 71·0–84·5 (M = 77·1) per cent of head. Pelvics with the first ray slightly produced.

Teeth. The *outer teeth* in both jaws are unequally bicuspid, with the major cusp obliquely truncate in most fishes, but especially so in larger individuals (text-fig. 30); both the crown and the neck of the tooth are compressed. Occasionally, the teeth situated posteriorly and posterolaterally in the premaxilla are tricuspid or unicuspid; this difference may be size correlated, with unicuspids commoner in larger fishes (i.e. > 55 mm standard length).

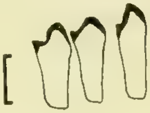

FIG. 30. *H. pappenheimi.* Dentary teeth (right), lateral and anterolateral in position. Viewed laterally. Scale = 0·25 mm.

The posterior quarter to third of the premaxilla is edentulous; there are 28–38 (M = 34) teeth on the rest of the bone.

Inner teeth are small, invariably tricuspid, and are arranged in a single row in both jaws. Sometimes in the upper jaw the row is irregular and gives the impression of being double.

OSTEOLOGY. The *neurocranium* of *H. pappenheimi* departs from the generalized *Haplochromis* type, approaching that found in *H. schubotzi* and *H. schubotziellus*, and in *H. guiarti* of Lake Victoria (*see above* p. 186, and Greenwood 1962).

The *lower pharyngeal bone* is fine, and its dentigerous surface is distinctly broader than long (1·25–1·30 times). The teeth are very fine, slender, compressed and cuspidate, and are closely arranged in from 30 to 34 rows. The posterior margin of the bone is noticeably concave in outline when viewed from above, having the shape of a shallow V.

Vertebral counts in the 8 specimens examined are 30 (f.3), 31 (f.4) or 32 (f.1), comprising 14 (f.6) or 15 (f.2) abdominal and 16 (f.4) or 17 (f.4) caudal centra.

COLORATION IN LIFE. There appears to be no marked sexual dimorphism in coloration, although the possibility of this occurring cannot be overruled because no sexually active males have yet been examined. However, large and adult males were caught in the Kazinga Channel and these did not differ from females, except in being slightly darker.

The ground colour in both sexes is silver, shot with green iridescence above the midlateral line, and whitish on the belly. All fins are hyaline, but in males the lappets of the dorsal fin are black, as are the pelvic fins. The anal fin of males carries from 1 to 3 yolk-yellow ocelli.

PRESERVED COLORATION. Ground coloration is greyish-silver, darker (i.e. greyer) on the dorsum and flanks to about the midlateral line. All fins are hyaline to greyish, the lappets of the spinous dorsal black in males, as are the pelvic fins.

Distribution. Lakes Edward and George and the Kazinga Channel.

ECOLOGY. *Habitat.* The slender body form and pelagic habits of this species have resulted in relatively few specimens being caught in the nets used by the I.B.P. team. Thus, not a great deal is known about the habitat preferences of *H. pappenheimi.* The species is apparently confined to upper water levels in offshore regions of the lake (both in bays and in the open lake). An intensive study of the species is now in progress. The use of purse-seine nets and small-mesh trawls should result in many more samples being taken.

Food. The few guts examined contained only zooplankton, particularly copepods and cladocerans.

Breeding. Most of the specimens on which this description is based are sexually immature, but 2 fishes (females, 60 and 61 mm standard length) show signs of ovarian activity. Obviously, adults of *H. pappenheimi* in Lake George must reach a larger size (as they do in Lake Edward and the Kazinga Channel). There is, of course, the possibility that adult individuals move out of Lake George, and that the breeding sites are in the Kazinga Channel. To date the only evidence (and that rather flimsy) supporting this hypothesis is the capture, in May 1972, of numerous large adults in the channel, when, using the same gear (a purse seine), only juveniles were collected in the Lake itself.

One of the paralectotypes from Lake Edward, a female (72 mm standard length) is brooding young in the buccal cavity, as are 2 females (72·0 and 69·0 mm standard length) in the paralectotypical series of the British Museum (Natural History). Unfortunately it is impossible to sex the other paralectotypes with any certainty. All are apparently female, the largest a fish 92·5 mm standard length.

DIAGNOSIS AND AFFINITIES. The species is immediately distinguishable from other Lake George *Haplochromis* species by its slender body form, head shape, by its long and slender caudal peduncle, and by the shape and distribution of its outer jaw teeth. In life the silvery blue-green coloration is also diagnostic.

There is an overall similarity between *H. pappenheimi* and *H. guiarti*, a species endemic to Lake Victoria but which was once thought to occur in Lake Edward (Trewavas 1933 ; but *see below* p. 232).

Haplochromis pappenheimi differs from *H. guiarti* in several characters ; for example, the dentition (obliquely cuspidate teeth, contrasted with the usual unicuspid and unequally but acutely bicuspid teeth of *H. guiarti* ; the fewer teeth in *H. pappenheimi*, and the fully toothed premaxilla of *H. guiarti* compared with the posteriorly edentulous bone of *H. pappenheimi*), a shallower preorbital (12·5–16·8, M = 14·8 per cent head, *cf.* 16·3–21·5, M = 18·3 per cent in *H. guiarti*), shorter snout (24·0–30·8, M = 28·1 per cent head, *cf.* 31·7–37·5, M = 34·4 per cent), larger eye (31·5–37·0, M = 33·4 per cent head, *cf.* 23·6–29·8, M = 26·5 per cent in *H. guiarti* of the same size), and a longer caudal peduncle (19·8–24·5, M = 22·2 per cent standard length, *cf.* 16·2–20·8, M = 18·9 per cent).

Among the Lake Victoria *Haplochromis* species there is only one other, *H. fusiformis* Greenwood & Gee, that resembles *H. pappenheimi*. *Haplochromis fusiformis* is confined to the deeper waters (90–100 ft) of the lake and is benthic in habits. Like *H. pappenheimi* it has a partly edentulous premaxilla and is slender bodied. Interspecific differences, however, are well marked and include a shallower body, deeper preorbital, smaller eye and longer lower jaw in *H. fusiformis*, as well as the retention of typical bicuspid teeth in that species.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 297–298	Kankurunga Island
1972.6.2 : 317–320	Small island north of Kankurunga Island
1972.6.2 : 328–332	Small island north of Kankurunga Island
1972.6.2 : 333–336	Small island north of Kankurunga Island
1972.6.2 : 337–342	Tufmac Bay

Haplochromis squamipinnis Regan, 1921

(Text-fig. 31)

Haplochromis squamipinnis Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 636 (a single specimen, the holotype, BMNH reg. no. 1914.4.8 : 32, from Lake Edward).

Haplochromis squamipinnis : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 338–339 (mostly Lake Edward fishes, but 1 from Lake George).

NOTE ON *H. mentatus* Regan 1925, A PUTATIVE SYNONYM OF *H. squamipinnis*. Trewavas (1933) noted that the holotype and only specimen of *H. mentatus* (a Lake Edward species) closely resembled *H. squamipinnis*. She was unable to examine the holotype and thus did not see fit to formally synonymize the species with *H. squamipinnis*.

During a recent visit to the Museum of Comparative Zoology, Harvard University, I was able to examine *H. mentatus* holotype (MCZ no. 31523), a small fish 94·0 mm standard length, of indeterminable sex. In all morphometric characters and in most anatomical features this specimen is, as Trewavas suggested, like a young *H. squamipinnis*. However, I could not find any trace of the minute scales which are closely adherent to the bases of the anal and dorsal fin rays of *H. squamipinnis*, irrespective of the individual's size (*see below* p. 206).

These scales, which extend for a short distance onto the fins, are delicate and easily dislodged. Furthermore, there is considerable individual variability with regard to the number and position of the fin rays with which the scale rows are associated. Despite this variation, however, I have yet to examine a specimen of *H. squamipinnis* in which there is absolutely no trace of fin scales.

Thus, it is difficult to assess the significance of their total absence in *H. mentatus* holotype, especially since in all other trenchant characters the specimen agrees with comparable-sized *H. squamipinnis*.

Personally, I would be inclined to consider it either a young *H. squamipinnis* in which all traces of fin scales rows are lost, or an aberrant member of the species in which these scales failed to develop.

DESCRIPTION OF *H. squamipinnis*. Based on 34 specimens 34·0–202·0 mm standard length, from Lake George (including the specimens collected by Worthington in 1931). Because most characters show some allometry with standard length, the sample has been divided into two groups, viz. : (a) fishes < 120 mm standard length and (b) fishes > 129 mm standard length. Ranges and means for the various morphometric characters are given accordingly.

Depth of body (a) 32·1–37·0 (M = 34·7), (b) 34·7–41·0 (M = 37·4) per cent of standard length, length of head (a) 33·5–37·6 (M = 35·4), (b) 33·9–36·2 (M = 35·0) per cent.

Dorsal head profile straight but broken by the prominent premaxillary pedicels, sloping at an angle of *ca* 40° with the horizontal.

Preorbital depth (a) 15·0–19·0 (M = 17·0), (b) 17·8–20·4 (M = 21·9) per cent of head, least interorbital width (a) 19·2–23·0 (M = 21·9), (b) 21·3–25·4 (M = 23·0) per cent ; length of snout equal to or slightly greater than its breadth in fishes of both size groups, but in (a) 30·8–33·8 (M = 32·3) per cent of head and in (b) 31·5–37·1 (M = 34·9) per cent.

Eye diameter (a) 23·0–33·0 (M = 27·5), (b) 21·2–25·5 (M = 23·0) per cent of head ; depth of cheek (a) 18·3–27·6 (M = 24·5), (b) 27·8–31·7 (M = 29·3) per cent. For the cheek depth and eye diameter the lowest and highest values respectively relate to the smallest specimen examined.

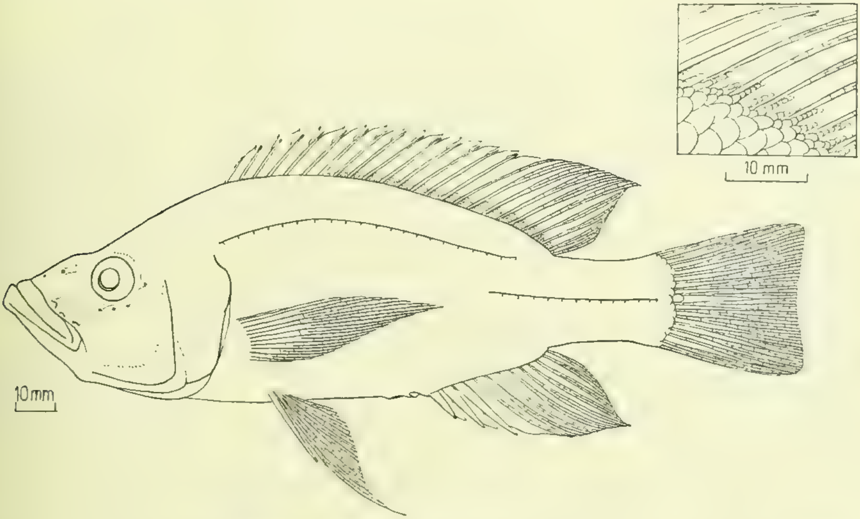

Fig. 31. *Haplochromis squamipinnis.* Lake George specimen. Inset shows squamation on dorsal fin.

Caudal peduncle not showing allometric growth, its length 14·7–20·6 (M = 16·8) per cent of standard length, 1·1–1·5 (modal range, 1·2–1·4) times as long as deep.

Mouth distinctly oblique, sloping upwards at an angle of *ca* 35–45 degrees to the horizontal. Jaws equal anteriorly or the lower projecting slightly (the usual condition). Length of lower jaw in (a) 41·8–53·8 (M = 47·5), (b) 47·3–56·6 (M = 51·3) per cent of head, length of upper jaw in (a) 33·3–40·0 (M = 37·0), in (b) 39·3–45·5

(M = 42·4) per cent, 1·1–1·5 (modal range 1·2–1·4) times longer than broad in both size groups. The smallest specimen examined (34·0 mm standard length) has, proportionately, the shortest jaws.

Posterior tip of the maxilla reaching a vertical through the orbital margin in most fishes, not quite reaching this level in a few, and extending beyond it to below the eye in others ; this variation does not seem to be size correlated.

Gill rakers. The lower 1–3 rakers are reduced, the remainder are relatively slender. In some specimens the uppermost 1 or 2 rakers may be flat and anvil-shaped, and in some individuals all the rakers are short and relatively stout. There are 8–11 (rare), usually 9, rakers on the lower part of the first gill arch.

Pseudorakers are poorly developed : the tissue lying between the inner and outer gill raker rows is thickened and slightly produced into ill-defined, low projections.

Scales. Ctenoid ; lateral line with 31 (f.1), 32 (f.17) or 33 (f.12) scales, cheek with 3, 4 (mode) or 5 rows. Five and a half to 7 (rare), usually 6, scales between the upper lateral line and the dorsal fin origin, 5–7 (mode 6) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.1), 15 (f.21) or 16 (f.9) spinous and 9 (f.19) or 10 (f.12) branched rays. Anal with 3 spines and 9 (f.22) or 10 (f.9) branched rays.

A peculiarity of both dorsal and anal fins is the presence of short vertical rows of minute scales extending from the body onto the fin (*see* text-fig. 31). The scales are closely applied to the fin rays, both spinous and branched. Not all rays have associated scale rows, and the distribution of the rows shows considerable individual variability. Most frequently, the entire soft part of the dorsal fin has basal scale rows, as does the entire soft anal. Generally the anterior part of the spinous dorsal is asquamous, the scale rows only beginning at about the sixth or seventh spine. However, the rows may begin as far forward as the fourth spine, or may not appear until the eleventh spine.

The scales are easily dislodged and part of this variability may be attributable to damage sustained when the fish is caught, especially if it has been trapped in a gill-net. No specimen was seen in which all the fin scale rows are missing, and the anal fin squamation is usually better preserved than that of the dorsal (another reason for thinking that damage during capture may account for some of the observed variability).

The caudal fin is truncate to weakly subtruncate, and is scaled on its basal half or a little more.

Pectoral fin length shows no marked allometry with standard length ; however, the relatively shortest fin is found in the smallest fish (34·0 mm standard length). Length of pectoral 23·5 30·0 (M = 28·1) per cent of standard length, 66·6–87·0 (M = 79·9) per cent of head.

Pelvic fins have the first ray produced and relatively more elongate in adult males than in females.

Teeth. Except for the smallest specimen (34·0 mm standard length), the predominant tooth form in the *outer row* of either jaw in fishes of 49·0–202·0 mm standard length is a slender but strong unicuspid with a slightly to strongly incurved crown. Some fishes in the size range 75–85 mm standard length have a few weakly and unequally bicuspid teeth interspersed among the unicuspids anteriorly and anterolaterally in both jaws; in one fish, most outer teeth in the lower jaw are bicuspid, although some typical unicuspids occur anteriorly. In fish of all sizes the posterior premaxillary teeth are unicuspid.

The 34 mm standard length fish has typically unicuspid teeth posteriorly and posterolaterally in the upper jaw, but unequally bicuspid teeth (the major cusp long and slender) anteriorly; all the lower jaw teeth in this fish are unicuspid and typical.

The number of outer premaxillary teeth is positively correlated with standard length; in fishes < 118 mm standard length there are 34 (in the smallest specimen) to 70 ($M = 48$) teeth, and in fishes > 130 mm standard length, 46–80 ($M = 60$) teeth.

Fishes > 90 mm standard length have the *inner tooth rows* composed of slender unicuspids, although in fishes as long as 100 mm some weakly tricuspid teeth may also occur. At lengths between 70 and 90 mm, there is usually an admixture of tri- and unicuspid teeth, but in some fishes only tri- and weakly tricuspids are found. In smaller specimens, tricuspids predominate.

OSTEOLOGY. The *neurocranium* in *H. squamipinnis* is of a relatively specialized type, both with respect to the basic *Haplochromis* neurocranial type, and also to the presumed basic skull form in piscivorous species (such as is shown by *H. guiarti*, *H. victorianus* and *H. serranus* of Lake Victoria, *see* Greenwood 1962, 1967). It compares closely with the neurocranial type found in Lake Victoria species like *H. longirostris* and *H. mento*, species that have deviated from the near basic *H. serranus* grade (Greenwood, *op. cit.*).

The *lower pharyngeal bone* is relatively fine and has an equilateral dentigerous area. The teeth are compressed, but strong, with weakly developed cusps and are somewhat sparsely distributed on the bone in *ca* 18–20 rows.

Vertebral counts in the 11 specimens radiographed are 29 (f.3) and 30 (f.8), comprising 13 (f.11) abdominal and 16 (f.3) or 17 (f.8) caudal elements.

COLORATION IN LIFE. *Adult males*: the ground colour is greyish with a turquoise to blue-green sheen covering most of the flank and caudal peduncle. The dorsal head and body surfaces are dark grey, the chest and belly greyish to greyish-sooty, the branchiostegal membrane sooty.

Dorsal fin dusky, darkest along its basal third, the upper margin of this dark area with a gently undulating outline; the lappets are black but there is a narrow, pinkish margin to the soft part of the fin. Deep orange-red spots occur between the posterior rays of the soft dorsal. Caudal fin dark hyaline, with deep red spots and a light red (almost pink) flush over the ventral half of the fin and at its upper and lower distal angles. Anal fin almost completely pink, but with a hyaline area around the yolk-yellow ocelli. The pelvic fins are black.

Females and immature males are golden-silver dorsally, shading to yellowish-green on the flanks, and to white on the belly and ventral flanks. Dorsal fin yellowish-green, becoming hyaline dorsally. The caudal is similarly coloured, but has dark spots over its proximal two-thirds. Anal fin dark hyaline basally, yellow-green distally ; females often have yellow spots in the position of the ocelli in males, but young males may lack any indications of such markings. The pelvics are hyaline or yellowish, becoming dusky in near-adult males.

Preserved coloration. *Adult males* : the ground colour is brownish-grey above, shading to silvery grey or dusky silver on the lower flanks and belly ; the chest is silvery or dusky silver. Upper surface of the snout and the lips (at least anteriorly) are dark grey, the lower jaw and branchiostegal membrane dusky grey. The only cephalic marking is an ill-defined lachrymal stripe.

The dorsal fin is grey, the lappets black. Basally there is a darker band (in places almost black) which widens over the soft part of the fin so that the basal third to half of the fin is black or very dark grey in colour. The distal part of the soft dorsal is densely and darkly maculate. The caudal is dark grey, most intensely so over its proximal third to half. The anal is grey to dusky grey, with the basal third noticeably darker. The pelvic fins are black.

Females and juvenile males are light brown above, shading to silvery yellow on the flanks and belly. The lips, snout and lower jaw are coloured as in adult males, but are slightly paler in some individuals. The lachrymal blotch is poorly defined but is generally visible. The coloration of the dorsal, caudal and anal fins is like that of adult males, but is more variable in its intensity. The pelvics are hyaline or a little dusky (more so in juvenile males) over the distal part of the first 3 rays.

Ecology. *Habitat.* At least when adult, individuals of *H. squamipinnis* are found in all habitats, but are especially common in the offshore open-water areas of the lake. Juveniles may have a more restricted distribution to areas nearer the shoreline.

Food. Fishes predominate in the diet of *H. squamipinnis* at all the growth stages investigated (70–200 mm standard length), and appear to be the sole food source of fishes more than 150 mm standard length. In small fishes insects contribute substantially to the diet.

As far as could be determined, the principal prey species are other *Haplochromis*, but the macerated nature of the gut contents in *H. squamipinnis* generally precludes accurate identification.

Breeding. Haplochromis squamipinnis is a female mouth brooder. All examined individuals less than 120 mm standard length are immature ; the first indications of sexual activity are found in fishes (of both sexes) in the size range 125–130 mm standard length.

Because all specimens larger than 155 mm standard length are females, there may be sexual dimorphism in the maximum adult size attained.

Of the 13 sexually active females examined, 5 have the right ovary larger than the left one, 2 have the right ovary slightly larger and 6 have the ovaries equally developed.

Distribution. Lakes Edward and George and the Kazinga Channel.

Diagnosis and affinities. The overall appearance of *H. squamipinnis* with its long and obliquely sloping jaws, its unicuspid teeth, and the peculiar scale rows on the median fins, immediately distinguishes this species from all known *Haplochromis* species in Lake George. The same criteria would distinguish it from all known *Haplochromis* species in Lake Edward, but a rather similar species is now known to occur in that lake (Greenwood, unpublished information).

Haplochromis squamipinnis resembles a number of piscivorous *Haplochromis* species in Lake Victoria, but none of these has scale rows on the fins.

Taken in concert, the cranial and dental characters of *H. squamipinnis* place it near *H. victorianus* and *H. serranus* (i.e. the '*serranus*' group of Greenwood 1967). However, in certain characters, especially skull form, *H. squamipinnis* approaches the rather more specialized structural grade seen in *H. mento* and *H. longirostris* (i.e. of the '*prognathus*' group as defined by Greenwood, *op. cit.*).

Despite the general and often particular resemblances between *H. squamipinnis* and these various Lake Victoria species, it can be distinguished from them by various combinations of morphometric characters. It may be significant, in phylogenetic terms, that the male coloration of *H. squamipinnis* is not markedly different from that of *H. victorianus* (*see* Greenwood 1962, p. 157), and that several Lake Victoria species of the '*serranus*' group show basically similar male breeding coloration.

Haplochromis squamipinnis also resembles *H. venator* Greenwood, the sole piscivorous *Haplochromis* species of Lake Nabugabo (Greenwood 1965b). Skull morphology in *H. venator* is rather more like that of *H. mento* than of *H. squamipinnis*, and there are some differences in gross body form as well as some specific morphometric ones (especially the deeper body and wider interorbital of *H. squamipinnis*). *Haplochromis venator*, of course, lacks the scale rows on its dorsal and anal fins. Certainly the similarities between this species and *H. squamipinnis* are no closer than those between *H. squamipinnis* and the Lake Victoria species considered above.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2 : 379	I.B.P. Jetty
1972.6.2 : 380	I.B.P. Jetty
1972.6.2 : 381–386	Kashaka Bay
1972.6.2 : 387–395	Various localities
1933.2.23 : 449	Collected by Worthington
1933.2.23 : 439–443	Collected by Worthington
1933.2.23 : 450–451	Collected by Worthington
1933.2.23 : 452–455	Collected by Worthington
1933.2.23 : 444–448	Collected by Worthington

Haplochromis petronius sp. nov.

(Text-figs. 32–34)

HOLOTYPE. A male 85·5 mm standard length, BMNH reg. no. 1972.6.2 : 1, from Kashaka Crater, Lake George.

The trivial name, from the Latin, meaning 'of, or pertaining to rocks', refers to the usual habitat of this species in Lake George.

DESCRIPTION. Based on 25 specimens, 67·0–88·0 mm standard length (including the holotype), all from Lake George.

Depth of body 33·2–38·3 (M = 35·8) per cent of standard length, length of head 31·8–35·8 (M = 33·8) per cent.

Dorsal head profile straight, sloping steeply at an angle of *ca* 50°–55° with the horizontal.

Preorbital depth 14·5–19·3 (M = 17·6) per cent of head, least interorbital width 19·2–25·0 (M = 22·1) per cent. Snout length 0·7 – 0·9 (mode 0·8) of its breadth, 28·0–34·6 (M = 31·2) per cent of head, diameter of eye 25·0–30·8 (M = 28·0), depth of cheek 24·5–30·2 (M = 27·2) per cent.

Caudal peduncle 12·6–16·8 (M = 15·7) per cent of standard length, 1·1–1·4 (modal range 1·2–1·4) times as long as deep.

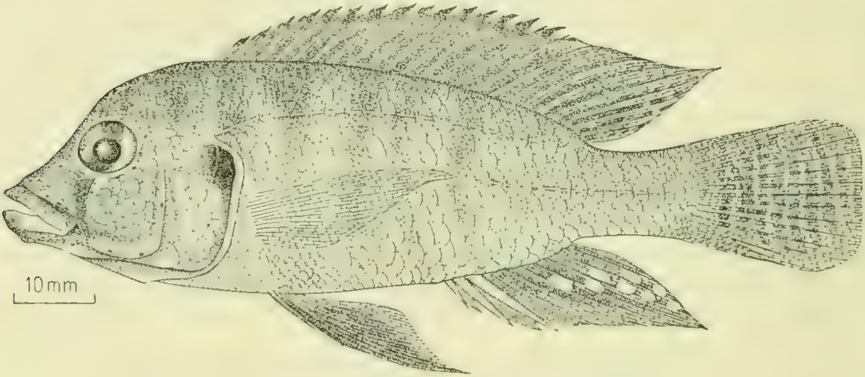

FIG. 32. *Haplochromis petronius*. Holotype.

Jaws equal anteriorly, mouth horizontal, the lips thickened. Posterior tip of the maxilla reaching a vertical through the anterior margin of the pupil, rarely not reaching so far posteriorly. Length of upper jaw 34·2–41·6 (M = 36·8) per cent of head, length of lower jaw 34·8–41·5 (M = 37·8) per cent, 1·3–1·7 (modal range 1·3–1·5) times its breadth.

Gill rakers. The lower 1–3 rakers of the first gill arch are reduced, the others are usually short and stout, but rather slender in some fishes. There are 7 or 8 (mode) rarely 9, rakers in the outer row on this arch.

The pseudorakers are very well developed and are transversely aligned so as to link the inner and outer rows of true gill rakers on the first arch.

Scales. Ctenoid ; lateral line with 30 (f.3), 31 (f.4), 32 (f.15) or 33 (f.2) scales, cheek with 3 or 4 rows. Scales on the nape and chest are small, the latter rather deeply embedded. The transition between the larger ventral belly scales and the much smaller thoracic scales is abrupt, and occurs at about the level of the pectoral fin insertion. This abrupt type of size transition is unusual in *Haplochromis* (*see* Greenwood 1971). Another unusual character of the squamation in *H. petronius* is the presence of a small naked area (equivalent to about 4 or 5 scales) immediately anterior to the insertion of the first dorsal fin spine.

There are 5–7 (mode 6) scales between the upper lateral line and the dorsal fin origin, and 7–10 (modal range 8–9) between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.3), 16 (f.21) or 17 (f.1) spinous and 8 (f.1), 9 (f.21) or 10 (f.3) branched rays. Caudal strongly subtruncate, almost rounded ; scaled on its basal third to half.

Pectoral fin 26·5–32·4 (M = 28·1) per cent of standard length, 75·0–97·8 (M = 82·0) per cent of head length. Pelvics with the first ray somewhat produced in both sexes.

Teeth. In the *outer row*, the teeth posteriorly in the premaxilla are unicuspid and caniniform ; anteriorly in this jaw and throughout the lower jaw the teeth are stout, unequally bicuspid (often weakly so), and have the crown incurved (text-fig. 33). These teeth are cylindrical in cross-section, with the upper part of the crown compressed. Occasionally, a few unicuspids occur anteriorly in the upper jaw, interspersed among the usual bicuspids. Also, in a few fishes the posterior premaxillary teeth are slender and bicuspid, not unicuspid as is usual for teeth in that position.

There are 36–50 (M = 42) teeth in the outer premaxillary row.

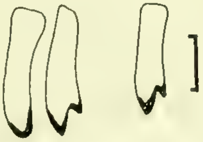

FIG. 33. *H. petronius.* Premaxillary teeth (left), anterolateral in position. Viewed laterally. Scale = 0·5 mm.

Inner teeth are usually tricuspids in fishes < 75 mm standard length (and in a few larger individuals) but most fishes > 75 mm long have an admixture of tricuspid, weakly tricuspid and unicuspid teeth. There are 2 or 3 rows of inner teeth in the upper jaw, and 2 (less frequently 3) in the lower jaw.

OSTEOLOGY. The *neurocranium* is of the generalized *Haplochromis* type (*see* p. 147) with a moderately decurved preorbital profile.

The *lower pharyngeal bone* is relatively stout, its dentigerous surface equilateral. The teeth are cuspidate and compressed, with those of the median rows noticeably coarser (text-fig. 34). In a few specimens some or all of the median teeth are submolariform. There are *ca* 20–24 rows of teeth.

Vertebral counts in the 12 specimens radiographed are 29 (f.10) and 30 (f.2), comprising 12 (f.1), 13 (f.10) or 14 (f.1) abdominal and 15 (f.1), 16 (f.8) or 17 (f.3) caudal centra.

COLORATION IN LIFE. *Males, adult but not sexually active* : the flanks are greenish-yellow, tinged with blue, the blue concentrated along the scale margins ; dorsally the colour changes to greenish-violet. The belly and chest are white, the branchiostegal membrane light grey. The lips are turquoise, and there are strong tinges of turquoise on the basically grey snout and cheeks.

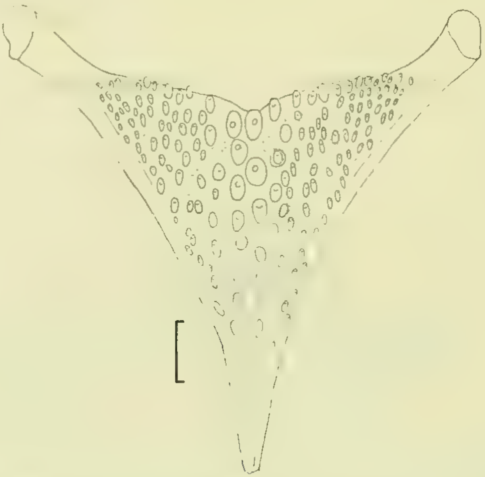

FIG. 34. *H. petronius.* Lower pharyngeal bone, occlusal view. Scale = 1·0 mm.

The dorsal fin is light sooty-grey, with the base greenish-blue, and the lappets red (as is the margin of the soft part); the soft part also has a scattering of well-marked, elongate, deep red streaks and spots. The anal fin is also sooty-grey (sometimes flushed with pink or red, perhaps a correlate of sexual activity) with a light-blue area along its base and a narrow scarlet outline to its margins; there are as many as eight bright orange ocelli on the posterior part of this fin. The caudal is dark grey, outlined in red, this marginal band expanding at the posterodorsal and ventral angles of the fin; deep maroon streaks occur between the rays. The pelvic fins are black or sooty, the spine and first ray are, however, bluish-white.

Females: no live females have been observed.

PRESERVED COLORATION. Only males are available, all are adult. The ground colour is uniformly light grey-brown; in some specimens there are traces of up to 7 dark but faint vertical bars across the flanks and caudal peduncle, those on the flanks extending from the dorsal body outline almost to the ventral body margin. The snout is dark grey to dusky, the lower jaw dusky-grey and the lips pale. The ventral aspects of the cheek and operculum are of variable duskiness, almost black in some fishes but only a dark brown in others. The branchiostegal membrane is greyish-sooty. Cephalic markings comprise a usually distinct and intense lachrymal stripe, and 2 transverse bars, of variable intensity, across the snout.

The dorsal fin is dark grey to sooty, the membrane between the last few branched rays maculate. The caudal is grey, maculate distally and dark grey, almost black basally. The anal fin is greyish to sooty, the pelvics variable, from dusky to black but with the spine and first ray much lighter.

ECOLOGY. *Habitat. Haplochromis petronius* is the only Lake George *Haplochromis* species that appears to have a clearly circumscribed habitat. With a few exceptions (*see below*) the species has been found only in a rocky bay situated immediately behind the village of Kashaka. This bay is an old volcanic crater, one wall of which has collapsed and thus connected the crater with the lake. The bay is roughly ovoid in outline, its greatest and least axes being about 1·3 and 0·8 km. At its centre the water is some 6 m deep, but around the margins it is between 1 and 3 m. This marginal area has a rough substrate composed of rocks and stones derived from the crater walls. Some plant debris (including dead trees) lies among the rocks which, in places, are also covered lightly by a thin slick of organic mud. The bay is sheltered from all directions and has a relatively narrow entrance.

Haplochromis petronius is found only over the marginal rocky area of Kashaka Bay ; nets set in the deeper central area, either at the bottom or floating at the surface, caught no *H. petronius*, although other fishes (both cichlid and non-cichlid), including species found inshore, were caught.

The species is common in catches from its habitat ; other *Haplochromis* species inhabiting the same region include *H. angustifrons*, *H. elegans*, *H. aeneocolor* and *H. schubotziellus*, but none occurs in such abundance as does *H. petronius*.

Outside Kashaka bay, *H. petronius* is rarely encountered ; it is probably significant in this connection that no other areas of the lake have a similar rock-boulder substrate. The very few *H. petronius* caught in the main lake are either from near the papyrus fringe over a mud-bottom or from over a sandy substrate on an exposed shore facing the lake centre.

Food. Insects, both larval and emergent, seem to be the commonest food organisms in the diet of *H. petronius*, but the sample I examined was small (20 specimens).

Breeding. The specimens I have examined are all males, and indeed I have been unable to catch any females, despite intensive fishing in the area. Thus, it would seem that there is a definite segregation of the sexes, and probably at all times of the year, itself an unusual phenomenon amongst *Haplochromis* species.

The smallest fish examined (67 mm standard length) is a ripening male, although another specimen 69 mm standard length is probably immature.

Distribution. Known only from Lake George.

DIAGNOSIS AND AFFINITIES. Taken in its totality, the appearance of *H. petronius* is highly characteristic, and readily distinguishes this species from other *Haplochromis* in Lake George. The small chest and nape scales, the abrupt size transition between the thoracic and ventral body squamation, and the small scaleless area before the first dorsal fin spine are trenchant diagnostic features.

However, these particular characters are also found in a species known from Lake Edward, viz. *H. pharyngalis* Poll (*see also* p. 177). The overall morphology of *H. pharyngalis* is also very like that of *H. petronius*, especially the steep head profile, the horizontal mouth with its thickened lips and the near-rounded caudal fin outline.

The principal interspecific differences are twofold. First, in *H. pharyngalis* the lower pharyngeal bone is greatly enlarged (massive in 1 of the 3 known specimens), and there are several rows of enlarged molariform or near-molariform teeth (*see* Poll 1939a, p. 46, fig. 26). Second, the nuchal and thoracic scales (particularly the former) are relatively smaller in *H. pharyngalis*. In addition, there are fewer (i.e. 6) gill rakers in *H. pharyngalis*, and there is a naked area, about 1 scale row deep, on the ventral margin of the cheek.

With only 3 specimens of *H. pharyngalis* available for comparison and with no information on their live colours, it is difficult to assess the precise relationship between the species. Certainly the differences in pharyngeal bone development (and correlated dental differences) and in the size and shape of the apophysis for the upper pharyngeal bones seem well marked. But, these are of similar nature to those distinguishing the George–Edward populations of *Astatoreochromis alluaudi* from those of Lake Victoria (*see* Greenwood 1959a, and especially 1965a). That *H. pharyngalis* shows a range of pharyngeal bone enlargement (even in only 3 specimens), and that *H. petronius* exhibits incipient molarization of the pharyngeal teeth, adds to the impression of close relationship between the species. The question can only be pursued when larger samples of *H. pharyngalis* are available.

An even closer resemblance exists between *H. petronius* and *H. wingatii* (Blgr.), a species of the Nile and Lake Albert (*see* Greenwood 1971 for a revision of this often misidentified species). Again, comparisons are hampered by the small number of specimens available. Only 2 well-preserved and 1 poorly preserved specimen of *H. wingatii* are known, all much smaller than the smallest *H. petronius* available, and there are no data on their live colours.

Morphometrically, *H. wingatii* and *H. petronius* are indistinguishable except for the longer pectoral fin in *H. petronius* (75·0–97·8, M = 86·4 per cent head length, *cf.* 65·0–66·5 per cent for *H. wingatii*) and a higher vertebral count (29 or 30, *cf.* 28). Two slight interspecific differences are the absence of a naked predorsal area in *H. wingatii* and the existence of a naked strip below the cheek scales in that species. There is also a difference in the dentition. In the holotype of *H. wingatii* (53 mm standard length) the majority of the outer teeth in both jaws are slender, strongly recurved unicuspids. The outer teeth in *H. petronius* are relatively coarser and, except in the largest fishes, are all bicuspid. Even in large individuals the predominant tooth form is the bicuspid. The two other *H. wingatii* specimens are smaller and do have bicuspid teeth (as is usual for small individuals of species with a unicuspid definitive dentition). The bicuspids in these specimens are slender (like the few bicuspids of the holotype) and thus are unlike the bicuspids of *H. petronius*.

Resemblances between *H. wingatii*, *H. petronius* and *H. pharyngalis* are striking, particularly since they involve, principally, details of squamation not found in other species of Lakes Edward, George or Victoria, or even in the fluviatile *Haplochromis* species of east Africa. Reduced pectoral and nuchal squamation is known from other *Haplochromis* and *Haplochromis*-like species, but in all these fishes it is associated with rheophilic habits (Greenwood 1954; Thys van den Audenaerde 1963). The habitats of the 3 species under consideration are far removed from the torrential, and thus it is difficult to attribute the resemblances in squamation to environmentally induced parallelism. If, therefore, the similarities are a reflection of phyletic affinity, then *H. wingatii*, *H. petronius* and *H. pharyngalis* would appear to be of a lineage distinct from all other *Haplochromis* in Lakes Victoria, Edward and George. The implications of this conclusion will be considered later (p. 235).

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.2. : 1 (Holotype)	Kashaka Crater Bay
1972.6.2 : 2–10 (Paratypes)	Kashaka Crater Bay
1972.6.2 : 11–21 (Paratypes)	Kashaka Crater Bay
1972.6.2 : 22 (Paratype)	North end of Kankurunga Island
1972.6.2 : 23 (Paratype)	Caught over sandy shallows
1972.6.2 : 788 (Paratype)	Kashaka Crater Bay
1972.6.2 : 811 (Paratype)	Kashaka Crater Bay
1972.6.2 : 293	Sandy shoal

Haplochromis eduardianus (Blgr.), 1914

(Text-figs. 35–37)

Schubotzia eduardiana Boulenger, 1914, in *Wiss. Ergebn. Deuts. Zentral-Afrika Exped., 1907–1908, Zool.* **3** : 258–259 (Lake Edward).
Schubotzia eduardiana : Regan, 1921, *Ann. Mag. nat. Hist.* (9), **8** : 639.
Schubotzia eduardiana : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 340.

All these references are to specimens from Lake Edward ; the species was not discovered in Lake George until recently.

NOTE ON THE ALTERED GENERIC STATUS OF THE SPECIES. Boulenger (1914) defined the monotypic genus *Schubotzia* solely on the basis of its dental morphology.

The outer jaw teeth are unusual (text-fig. 36). The crown is somewhat expanded relative to the cylindrical neck, has the tip distinctly rounded and strongly incurved so as to lie almost horizontally. In outline (i.e. as a flattened object) the tooth is paddle-shaped.

The inner teeth, by contrast, are typical tricuspids but are restricted to 1 or 2 rows in each jaw.

In other characters, *Schubotzia* does not differ from *Haplochromis*. The lower jaw, especially the dentary, is deep and stout, and the premaxilla is rather inflated. However, both these characteristics can be seen in other *Haplochromis* species (e.g. *H. nigricans* and *H. obesus* of Lake Victoria), although the condition could not be described as a common one ; it is usually associated with a specialized dentition. The lower jaw of *Schubotzia* is slightly overhung by the upper jaw, again an unusual condition but one found in some *Haplochromis* species (e.g. *H. xenognathus* of Lake Victoria, a species with an unusual dentition, albeit one quite unlike that of *Schubotzia eduardiana* ; *see* Greenwood 1957).

The teeth of *Schubotzia* are outstandingly different when compared with those of other Lakes Edward and George cichlids (text-fig. 36) and especially with those of the

Haplochromis species known to Boulenger in 1914. But, when the *Schubotzia* tooth type is seen against the wide range of tooth morphology found within the genus *Haplochromis* as a whole (or just a segment like the species of Lake Victoria), then it does not seem to be so unusual.

In my opinion, the morphological differences separating *Schubotzia* from *Haplochromis* are relatively slight, and certainly less than those distinguishing *Haplochromis* from the Lake Victoria monotypic genera *Hoplotilapia* and *Platytaeniodus* (or those genera from one another).

To retain *Schubotzia eduardiana* in a separate and monotypic genus serves only to hide its close phyletic relationship with *Haplochromis*. Thus, I would favour classifying this taxon with its closest relatives, that is in the genus *Haplochromis*.

Rosen and Bailey (1963, p. 6) have succinctly stated the pragmatic and theoretical difficulties associated with the generic concept. Particularly they stress the often phyletically misleading results of undue emphasis placed on one or two outstanding morphological differences as generic criteria. I am fully in agreement with these authors' support for a wider use of the subgenus to indicate morphological divergence without losing sight of phyletic relationships. Reducing the genus *Schubotzia* to subgeneric status could well meet the requirements of this particular case. However, there is a great need for new and careful consideration of the generic and infrageneric classification of the ' genus ' *Haplochromis* as currently defined. Such a study must be based on phyletic principles and must test the phyletic integrity of what might well be a polyphyletic taxon.

It is my intention to undertake just such a study ; for the moment, I prefer not to establish *Schubotzia* formally as a subgenus of *Haplochromis*.

LECTOTYPE. A specimen 71·0 mm standard length, BMNH reg. no. 1914.4.8 : 35, from Lake Edward. This specimen is eviscerated and its sex cannot be determined ; the absence of dark pigment on the body suggests that it is a female (*see below* p. 220).

Three paralectotypes are in the collections of the Berlin Museum ; all are from Lake Edward.

DESCRIPTION. Based on 20 specimens, 50·5–79·0 mm standard length, from Lake George. A smaller fish, 35 mm standard length is not included in the morphometric section, since it is distorted, but certain features of its dentition are considered on p. 218.

Depth of body 30·5–36·7 (M = 33·5) per cent of standard length, length of head 31·5–34·3 (M = 33·1) per cent.

Dorsal head profile gently decurved, but sometimes straight, sloping at an angle of 30°–35° with the horizontal.

Preorbital depth 11·2–15·4 (M = 13·3) per cent of head, least interorbital width 23·0–28·3 (M = 25·9) per cent. Length of snout 0·8–0·9 of its width, 23·0–28·3 (M = 25·9) per cent of head, eye diameter 29·6–36·0 (M = 32·8) per cent, depth of cheek 16·7–22·2 (M = 20·0) per cent.

Caudal peduncle 14·7–19·5 (M = 16·9) per cent of standard length, 1·2–1·7 (modal range 1·3–1·5) times longer than deep.

Mouth horizontal, lips slightly thickened ; lower jaw shorter than the upper when the mouth is closed. Length of upper jaw 30·8–36·0 (M = 32·8) per cent of head, length of lower jaw 29·2–35·1 (M = 33·1) per cent, 1·0–1·4 (mode 1·1) times longer than broad. Posterior tip of the maxilla reaching a vertical through the anterior margin of the eye, rarely not quite reaching that level.

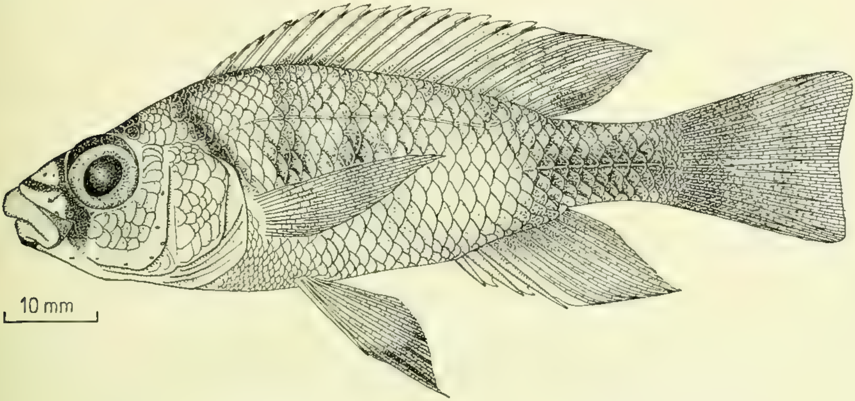

FIG. 35. *Haplochromis eduardianus.* Lake George specimen ; a male.

Gill rakers. The lowermost 1 or 2 rakers are reduced, the others are relatively slender although as many as 3 of the lower rakers may be relatively stout. The pseudorakers are well developed and prominent, but are short and stout.

There are 8 or 9 (rarely 10) gill rakers in the outer series on the lower part of the first gill arch.

Scales. Ctenoid ; lateral line with 31 (f.8), 32 (f.11) or 33 (f.1) scales, cheek with 2 or 3 (mode), rarely 4 rows. Five to 7 (modes at 5 and 5½) scales between the upper lateral line and the dorsal fin origin, 6–8 (mode 7) between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 (f.1), 15 (f.11) or 16 (f.8) spinous and 8 (f.6), 9 (f.13) or 10 (f.1) branched rays. Anal with 3 spines and 7 (f.2), 8 (f.16) or 9 (f.2) branched rays. Pectoral fin 26·5–32·4 (M = 28·1) per cent of standard length, 80·5–98·0 (M = 82·0) per cent of head. Caudal subtruncate, scaled on its basal half. Pelvics with the first ray slightly elongate.

Teeth. With one exception in the material studied, the shape of the *outer teeth* in both jaws is remarkably uniform. Each tooth is unicuspid, with a flattened crown that is almost half the total length of the tooth. The whole crown is strongly incurved (especially in teeth situated anteriorly and anterolaterally), and its tip is broadly rounded (text-figs. 36 & 37). The neck of the tooth is cylindrical and, compared with that of a typical bicuspid tooth, much stouter. If a tooth were straightened out so that the crown and neck are in one plane, then it would have the outline of a paddle.

The exceptional specimen mentioned earlier (a fish 50·5 mm standard length) differs from the others only in having a few small tricuspid teeth intercalated among the typical teeth posterolaterally in the upper jaw.

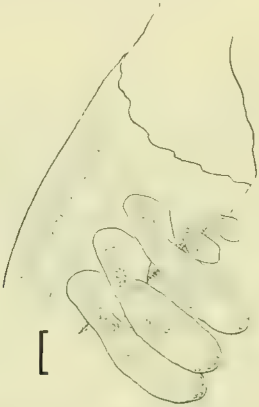

FIG. 36. *H. eduardianus.* Premaxillary teeth (right) anterior in position. Viewed from below and a little laterally, to show labial aspect of the teeth. Scale = 0·25 mm.

In the smallest available specimen (35 mm standard length), most teeth are like those of larger fishes, but in both jaws there are a few teeth with traces of a small lateral cusp. This minor cusp is not separated from the major one by a distinct gap, as in typical bicuspids. Instead, the demarcation between cusps is more in the nature of a narrow, V-shaped groove. Because a minor cusp is present, the outline of these teeth is not rounded but is rather bluntly oblique. Posteriorly in the lower jaw of this small fish there are a few tricuspid teeth.

There are 40–52 (M = 48) teeth in the outer row of the upper jaw ; the number not showing any correlation with the fish's size.

Inner teeth (text-fig. 37) in both jaws are tricuspid, with the crown compressed and strongly incurved ; arranged in 2 or rarely 3 rows in the upper jaw and a single (rarely double) row in the lower jaw. Virtually no interspace exists between the outer tooth row and the first row of inner teeth.

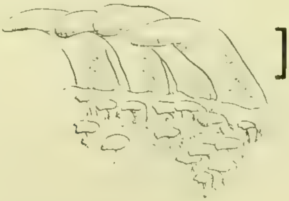

FIG. 37. *H. eduardianus.* Dentary teeth (left), anterolateral in position. Viewed from medial aspect to show lingual face of teeth. Scale = 0·25 mm.

OSTEOLOGY. The *neurocranium* is of the generalized *Haplochromis* type with a moderately decurved preorbital profile ; that is, a skull of the type found in *H. limax* and *H. petronius* rather than of the type in *H. macropsoides* and *H. elegans.* The premaxilla is a stout and inflated bone (especially the dentigerous arm) and resembles a more extreme form of the premaxilla found in *H. limax.* Stoutness and compactness also characterize the lower jaw. Both dentary and articular are stout, deep bones, and elements of the suspensorium are so arranged and proportioned that the dentary tip lies behind the vertical through the premaxillary symphysis. Presumably the general stoutness of the jaws is at least partly correlated with the presence of stout teeth.

The *lower pharyngeal bone* is relatively stout, although its teeth are fine (except for a few coarser posterior teeth in the middle tooth rows of larger fishes). There are *ca* 24–26 rows of teeth arranged over a dentigerous area about 1·3 times broader than it is long.

Vertebral counts in the 10 specimens radiographed are 29 (f.7) and 30 (f.3), comprising 13 (f.7) or 14 (f.3) abdominal and 15 (f.2), 16 (f.6) or 17 (f.2) caudal elements.

COLORATION IN LIFE. *Adult males* have a silvery blue-grey ground coloration, shading to white on the thoracic region ; many flank scales have deep red-brown centres, the intensity of the colour and the number of reddened scales correlated with the degree of sexual activity. Dark cephalic markings are always well developed. A thin stripe crosses the snout at the level of the lower orbital margin, and a much broader band runs between the upper orbital margins. Often this upper band is interrupted medially. A broad lachrymal stripe is continued above the eye as a wide blotch, the blotches from each side usually meeting medially. Behind this mark is another, this time in the form of a broad band crossing the nape from an origin at about the level of the upper opercular margin's midpoint.

The dorsal fin is hyaline with bright scarlet lappets and a diffuse scarlet flush between the spines ; this flush becomes concentrated into discrete blotches and spots between the branched rays. The anal is dusky on its proximal half, pinkish to scarlet distally ; the almost round ocelli (1 or 2) are very large and are yolk-yellow in colour. The caudal is entirely suffused with bright scarlet, although its ground colour is greyish-green. The pelvic fins are dusky but have scarlet streaks between the rays posteriorly on the proximal half of the fin.

Females (*at all stages of sexual activity*) : the ground colour is dark silver-grey shading to white on the belly and chest. Cephalic markings are usually absent, but if visible are a faint replica of those in the male (*see above*). The dorsal fin is hyaline, with a narrow scarlet marginal band on the soft part, and thin red streaks on the lappets of the spinous part ; in some individuals red streaks are present between the spines and rays. The caudal is hyaline with an overall pink flush, sometimes intensified to scarlet streaks between the rays and along the posterior margin of the fin. The anal is very pale yellow, with 2 deeper yellow spots (not ocelli) in the position of ocelli in males. The pelvics are whitish-hyaline.

PRESERVED COLORATION. *Adult males* : the ground colour is silver-grey, the flanks crossed by up to 10 vertical bars of variable intensity and definition ; the first 2 bars lie immediately behind the opercular margin, the last on the caudal peduncle. Dorsally, the bars extend to the body outline and at least anteriorly may extend onto the dorsal fin membrane ; ventrally the bars do not reach much below the level of the pelvic fin insertion.

Cephalic markings are very intense. Across the snout are 2 parallel bars, the upper generally twice the width of the lower. A broad lachrymal stripe is present, and there is a well-defined bar or triangular blotch extending towards the midline immediately behind the orbit. Posterior to this mark is another, but strap-shaped one which lies anterior to the dorsal fin origin. This bar appears to be a medial extension of the first vertical bar on the flank.

All fins, except the pectorals and pelvics, are yellowish, the basal region of the caudal often dusky. The pectorals are hyaline, and the pelvics black on the outer third, otherwise dusky.

Females are silvery grey or yellowish, with all fins yellow or hyaline. No cephalic markings are visible except, in some specimens, for a faint darkening below the eye, that is, in the position of a lachrymal stripe.

ECOLOGY. *Habitat.* The species is found in most inshore areas of the lake, over sand and mud bottoms, and in both exposed and sheltered localities. It has also been caught in the near-shore areas of the open lake but not further than about 100 m from the nearest land (in this case a small, reed-fringed island). No specimens have been collected in midlake or other distinctly offshore regions.

Food. The diet of *H. eduardianus* is still unknown. Most specimens examined had nothing recognizable except for a few sand grains and a few macrophyte fragments in any part of the gut.

The highly specialized dentition would suggest equally specialized feeding habits. By analogy with the similarly shaped teeth of *Plecodus* spp., one might suspect a similar diet of fish scales (Marlier & Leloup 1954).

Since the intestine of *H. eduardianus* is short (about half the length of the body) a vegetarian diet is almost certainly ruled out.

As so many (*ca* 90 per cent) of the specimens examined have nothing in the guts it seems probable that, whatever the food, it is rapidly digested.

Breeding. Haplochromis eduardianus is a female mouth brooder. Sexual maturity is reached at a standard length of *ca* 55 mm, and both sexes attain the same maximum length.

All of the 9 sexually active females examined have the right ovary much larger than the left one, and in some individuals only the right ovary is developed.

Distribution. Lakes Edward and George and the Kazinga Channel.

DIAGNOSIS AND AFFINITIES. *Haplochromis eduardianus* is distinguished from all other *Haplochromis* species in Lakes George and Edward by the morphology of its teeth. This peculiar tooth form led Boulenger (1914) to place the species in a distinct and monotypic genus. Reasons for not accepting Boulenger's classification are discussed above (p. 215). In essence, I argue that to place *H. eduardianus* in a monotypic genus (i.e. *Schubotzia*) is to obscure its phyletic relationships. That the dentition (both oral and pharyngeal) of *Haplochromis* group cichlids is, in an evolutionary sense, easily modified can be seen readily amongst the component species of the Lake Victoria *Haplochromis* species flock (*see* Greenwood 1965c for summary and further references). Indeed, in at least one instance the morphological sequence leading from generalized to highly specialized dentitions is still preserved among the extant species of that lake (Greenwood 1957). There are also examples where intraspecific variability is such that if only the extreme condition was known, and the criteria for generic status were based solely on morphological ' gaps ', then the species would have to be accorded generic status (*see* Greenwood, *op. cit.*, p. 96, with reference to *H. xenognathus*).

The reality of a morphological gap like that between the *H. eduardianus* tooth form and the shape of the teeth in any other *Haplochromis* species cannot be denied ; the difficulty lies in attempting to interpret the significance of the gap. The existence within a single species flock of such examples as *H. xenognathus* (and others where different species bridge a morphological gap) warns against hasty action that could obscure the essence of a phyletic classification ; that is, the demonstration of relationships as well as divergence. Is there any reason to suppose that, phylogenetically, the current evolutionary end-point seen in '*Schubotzia*' *eduardiana* and *Platytaeniodus degeni* or *Hoplotilapia retrodens* (both Lake Victoria monotypic genera ; *see* Greenwood 1956a) is any different from that represented by *H. xenognathus*? Certainly all three monotypic genera have as their nearest relatives a species of *Haplochromis*. That such a species can be found for *H. xenognathus* (Greenwood 1957) but not for *Schubotzia, Playtaeniodus* or *Hoplotilapia* may be more a reflection of a past epigenetic situation than of phyletic history.

STUDY MATERIAL

Register number BMNH	*Locality* : Lake George
1972.6.5 : 1–3	Tufmac Bay
1972.6.5 : 4	Kashaka Crater
1972.6.5 : 5–7	Small island north of Kankurunga Island
1972.6.5 : 8–13	Various localities
1972.6.5 : 14–20	Various localities

NON ENDEMIC *HAPLOCHROMIS* AND *HAPLOCHROMIS*-GROUP SPECIES IN LAKE GEORGE

Haplochromis nubilus (Blgr.), 1906

(Text-fig. 38)

Haplochromis nubilus (part) : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 329.

Most of the Lake George specimens referred to *H. nubilus* by Trewavas (1933) were misidentified, but two specimens (BMNH reg. nos. 1933.2.23 : 285–286) from Worthington's (1932) station 618 appear to be of this species. They are not included in the description given below.

Four specimens collected by the I.B.P. team can be identified with certainty since all are sexually active males and their live colours were recorded. These fishes came from a catch made close inshore, near reeds, in a bay of Akika Island.

A summary of morphometric characters is given below. It is based on 3 specimens only because the fourth is distorted and damaged. The latter specimen is, however, used in the description of the teeth and for fin ray and scale counts.

S.L.	Depth †	Head †	PO %	IO %	Snt %	Eye %	Cheek %	Lj %	Uj %	CP †
67·0	37·3	34·3	17·4	21·7	28·3	30·3	21·8	34·8	34·8	16·4
70·5	39·3	34·1	16·7	27·0	31·3	29·2	22·9	37·5	37·5	16·5
74·5	37·5	34·2	15·6	24·7	28·4	27·4	23·5	39·1	35·3	16·1

† = per cent of standard length.
% = per cent of head.
Lj = lower jaw, Uj = upper jaw.

Caudal peduncle 1·3–1·4 times longer than deep.

Dorsal head profile sloping steeply at *ca* 40°–45° with the horizontal, its outline straight except for a marked concavity above the orbital region. Upper margin of the orbit distinctly below the level of the dorsal profile.

Mouth horizontal, lips somewhat thickened; posterior tip of the maxilla reaching a vertical through the anterior margin of the orbit. Jaws equal anteriorly, the lower *ca* 1·3 times longer than broad. Snout slightly broader than long.

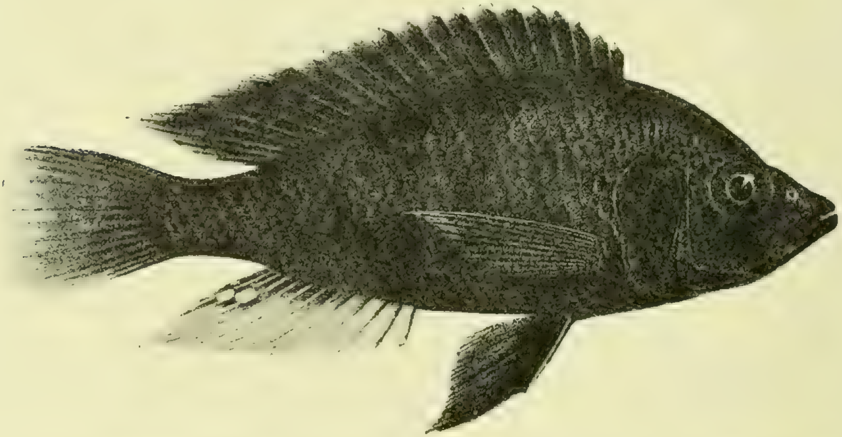

FIG. 38. *Haplochromis nubilus.* A Lake Victoria specimen. From Boulenger, *Fishes of the Nile.*

Gill rakers. Eight or 9 on the lower part of the first arch; the lower 2 rakers are reduced, the remainder are relatively stout. Pseudorakers are present and discrete, but are rather low and small.

Scales. Ctenoid; lateral line with 31 (f.2) or 32 (f.2) scales, cheek with 3 or 4 rows. Five or 5½ scales between the upper lateral line and the dorsal fin origin, 6 between the pectoral and pelvic fin bases.

Fins. Dorsal with 15 (f.4) spinous and 9 (f.2) or 10 (f.2) branched rays, anal with 3 spines and 8 (f.2) or 9 (f.2) branched rays. Pectoral 26·2–28·2 per cent of standard length, 76·5–83·3 per cent of head. Pelvics with the first ray variably produced, markedly elongate in one fish. Caudal distinctly subtruncate, almost rounded; scaled on its basal third to half.

Teeth. Posteriorly in the upper jaw the *outer teeth* are large and unicuspid. Elsewhere in this jaw, and throughout the lower jaw, the teeth are unequally bicuspid and moderately stout, or are an admixture of such teeth with slender unicuspids. Bicuspid teeth have the major cusps equilateral in outline and barely incurved; some teeth have faint indications of a flange on one aspect of the cusp (*see* p. 151).

There are 40–44 teeth in the outer premaxillary row.

Inner teeth in both jaws are small and tricuspid, are arranged in 2 or 3 rows in the upper jaw, and in 1 or 2 rows in the lower.

OSTEOLOGY. The *syncranium* of *H. nubilus* is typically that of a generalized *Haplochromis* species.

The *lower pharyngeal bone* is relatively slender, its teeth compressed and bicuspid, with those of the median rows slightly coarser (especially posteriorly). There are *ca* 24–28 rows of teeth arranged on a dentigerous area that is *ca* 1·2–1·3 times broader than long.

Vertebral count is 29 (comprising 13 abdominal and 16 caudal centra) in the 4 fishes radiographed.

COLORATION IN LIFE. *Adult males* have a highly characteristic velvety-black coloration that is virtually uniform over the whole body. The dorsal fin also is black except for a narrow scarlet margin along its entire length, and some scarlet spots and streaks on the soft part. A scarlet flush covers most of the anal fin, although the spinous part may be a little dusky; the ocelli are yolk-yellow. Proximally the caudal fin is black, and this dark colour may extend along the centre of the fin almost to its margin. The margin is bright scarlet, the colour expanding at the posteroventral margin of the fin. The pelvics are jet black.

The live colours of *females* from Lake George are unknown; in Lake Victoria the body is deep olive-green and all the fins are greyish-green.

Preserved males are either uniformly black on the body or the dorsum (above the midlateral line) may be lighter (i.e. a deep brown) and crossed by 4 or 5 rather faint vertical bars. The dorsal fin is black except for a pale (yellowish-orange) margin. Almost the entire anal is pale yellow, although there is a faint and narrow dark band basally. The caudal is dark proximally and between the middle rays, but otherwise it is yellowish. The pelvics are black.

ECOLOGY. Little can be said about *H. nubilus* in Lake George. The specimens I examined came from a shallow inshore area close to emergent vegetation. A similar habitat seems to be the preferred one for *H. nubilus* in Lakes Victoria and Nabugabo (Greenwood 1965b).

No data are available on the feeding and breeding habits of the species in Lake George. Lake Victoria populations are female mouth brooders, and have a rather omnivorous diet in whichv laral insects and small Crustacea predominate.

Distribution. Lakes Victoria, Kyoga, Nabugabo, Edward and George, and in many rivers and streams connected with these lakes. To date no specimens have been caught in the Kazinga Channel.

DIAGNOSIS. Morphologically, *H. nubilus* closely resembles *H. aeneocolor* (*see* p. 154) in nearly all characters, especially morphometric ones. Pseudorakers are present in *H. nubilus* but not in *H. aeneocolor*, and the caudal fin is virtually rounded in *H. nubilus* (but truncate in *H. aeneocolor*).

There are some dental differences between the species but these are not particularly trenchant. However, in *H. nubilus* flange development on the major cusp is certainly less common than in *H. aeneocolor*, and the flange, when developed, is less prominent. Also, judging from Lake Victoria *H. nubilus*, it seems probable that unicuspid outer teeth occur more frequently in this species than in *H. aeneocolor*.

In life, male breeding coloration is certainly diagnostic.

ASTATOREOCHROMIS Pellegrin, 1903

This genus is readily distinguished from *Haplochromis* by the higher number of anal fin spines : 4 or more, usually 5.

For a full diagnosis of the genus *see* Greenwood 1959a and 1965a, b.

Astatoreochromis alluaudi Pellegrin, 1903

(Text-fig. 39)

Astatoreochromis alluaudi : Trewavas, 1933, *J. Linn. Soc.* (*Zool.*), **38** : 321 (1 specimen from Lake George).

Astatoreochromis alluaudi occidentalis Greenwood, 1959, *Bull. Br. Mus. nat. Hist.* (Zool.), **5** : 174–175.

Very few specimens of *A. alluaudi* have been collected from Lake George by the I.B.P. team, despite an intensive fishing effort. Four specimens (45–104 mm standard length) are available for study.

Because *A. alluaudi* is easily recognized by its having 4 or more anal spines and greatly enlarged pharyngeal bones, and because the Lake George fishes do not differ greatly from those described elsewhere (Greenwood 1959a) no full description is necessary.

The live colour of Lake George fishes (previously unknown) is identical with that described for the Lake Victoria populations (*see* Greenwood, *op. cit.*, p. 172).

The lower pharyngeal bone and dentition of *A. alluaudi* from Lakes Edward and George are much less massive than those from comparable-sized fishes in Lake Victoria. This led me to describe a subspecies, *A. a. occidentalis*, for these western lakes (Greenwood 1959a). Subsequent research, however, strongly suggests that the degree of pharyngeal bone development (and of tooth molarization) is probably under direct environmental control (Greenwood 1965a). In other words, the differences between Lake Victoria and Lake Edward–George fishes is not genetically determined. Thus it seems inadvisable to continue recognizing two subspecies.

Lower pharyngeal bones and teeth in the 4 Lake George fishes fit broadly into the reductional pattern described for fishes from lakes other than Victoria and Kyoga

(Greenwood 1959a). However, the Lake George fishes seem to have rather more massive bones (and greater molarization of the teeth) than do fishes from Lake Nakavali. In the two smallest Lake George specimens (45 and 46 mm standard length) the bone is only a little less developed than in a comparable-sized specimen from Lake Victoria, and there is equal molarization of the teeth (*see* fig. 3 top right, in Greenwood 1959a). The 80 mm standard length Lake George fish has a bone comparable with that of the 123 mm standard length Lake Nakavali specimen figured (*op. cit.*), but the 104 mm standard length fish has a relatively less massive bone which is comparable with the same specimen from Lake Nakavali.

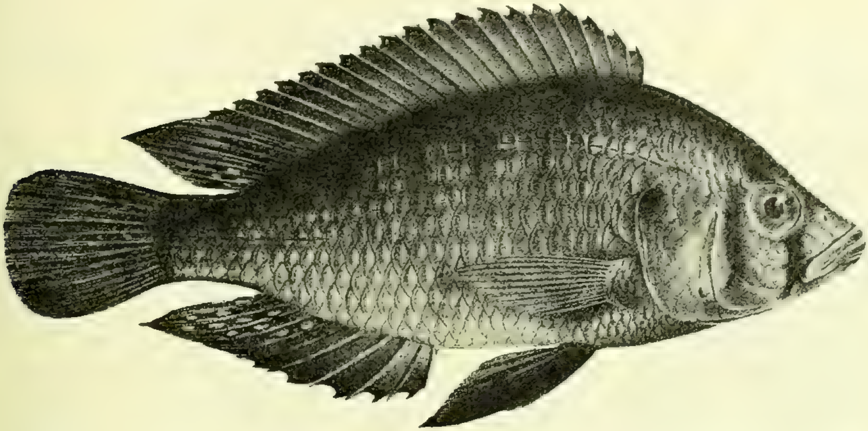

FIG. 39. *Astatoreochromis alluaudi.* A Lake Victoria specimen. From Boulenger, *Fishes of the Nile.*

The ratio of head length to pharyngeal bone width (measured from tip to tip of the upper arms) is in the range 2·9–3·0 (*see* Greenwood, *op. cit.*).

Vertebral counts for the 4 specimens are 13 + 16 (f.2), 13 + 15 (f.1) and 14 + 15 (f.1).

ECOLOGY. Little more can be added to our knowledge of this species in Lake George. The 4 specimens came from different areas of the lake, but a common feature for each locality is its proximity to the shore and the presence of rooted aquatic vegetation in the area.

Only fragments of gastropod shells were found in the intestines of the larger fishes (80 and 104 mm standard length); the 2 smaller individuals (45 and 46 mm standard length) yielded fragmentary remains of chironomid larvae.

HEMIHAPLOCHROMIS Wickler, 1963

The primary generic distinction of this superficially *Haplochromis*-like taxon is its reproductive biology (*see* Wickler 1963).

The two morphological characters that separate it from *Haplochromis* (at least those species occurring in Uganda) are:

(i) The typical elongate and raised cover to the lateral line canal opening in each pore scale on the body is absent from many of these scales in *Hemihaplochromis*. Instead there is either a simple pore or seemingly no opening at all ; scales in the posterior part of the upper lateral line series and those of the entire lower line are those most often missing a cover.

(ii) In males, instead of there being well-developed ocelli on the anal fin, there is a bright orange spot at the posteroventral angle (or tip) of the fin. This character is, of course, associated with the different reproductive behaviour of species in this genus (Wickler, *op. cit.*).

Hemihaplochromis multicolor (Schoeller), 1903

(Text-fig. 40)

For a full synonymy of this species, *see* Greenwood 1965b.

Only 1 specimen has been collected by the I.B.P. team. This apparent scarcity of *H. multicolor* in collections from the lake is probably a reflection of the small adult size attained and the habitats occupied, rather than a true indication of its abundance. Trewavas (1933) does not record *H. multicolor* from either Lake George or Lake Edward, and the only record from the Kazinga Channel is a few specimens I caught (by dip-netting amongst reeds) near Katungura (unpublished information).

The Lake George fish (BMNH reg. no. 1972.6.5 : 21) is 32 mm standard length and was caught near Busatu Island ; its sex is indeterminable.

Depth of body 35·9 per cent of standard length, length of head 35·9 per cent.

Dorsal head profile very gently curved, sloping at an angle of *ca* 40° with the horizontal.

Preorbital depth 17·4 per cent of head, least interorbital width 30·3 per cent, snout length 0·8 of its breadth and 26·0 per cent of head ; eye diameter 30·3 per cent of head, cheek depth 26·0 per cent.

Caudal peduncle as long as deep, 15·6 per cent of standard length.

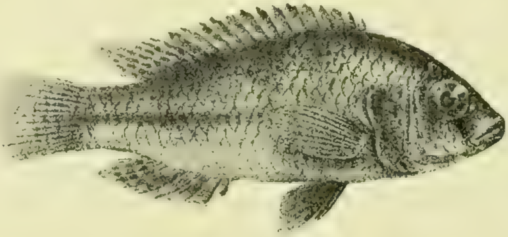

FIG. 40. *Hemihaplochromis multicolor*. A Lake Victoria specimen. From Boulenger, *Fishes of the Nile*.

Mouth slightly oblique, lips not thickened. Upper jaw 30·3 per cent of head, lower jaw 34·8 per cent. Posterior tip of the maxilla not quite reaching a vertical through the anterior orbital margin.

Gill rakers all short and stout, the lower 3 a little shorter than the others ; 7 rakers on the lower part of the first gill arch.

Scales. Ctenoid ; 29 in the lateral line series. Many of these scales (particularly in the lower series and posteriorly in the upper series) lack the longitudinal, arched cover to the pore opening, which is represented by a simple pit ; other scales are without any visible opening at all.

Cheek with 2 rows of scales ; 5 scales between the upper lateral line and the dorsal fin origin, 3 between the pectoral and pelvic fin bases.

Fins. Dorsal with 14 spines and 10 rays, anal with 3 and 9. Pectoral 23·4 per cent of standard length, 65·2 per cent of head length. Caudal fin rounded, scaled over slightly more than its proximal third.

Teeth. Posteriorly in the upper jaw, the *outer teeth* are very slender and unicuspid. Elsewhere in this jaw, and in the entire outer row of the lower jaw, the teeth are stout and unequally bicuspid. The major cusp is somewhat oblique in outline. There are 34 teeth in the upper jaw outer series.

Inner teeth are slender, slightly curved and unicuspid, and are arranged in a single row in each jaw.

Vertebral count. Thirteen abdominal and 16 caudal vertebrae.

ECOLOGY. Nothing is known about the bionomics of this species in Lake George. It seems probable (by analogy with its behaviour elsewhere) that in Lake George *H. multicolor* lives among submerged plants and in open-water areas within the margin of papyrus swamps (*see* Greenwood 1965b).

Hemihaplochromis multicolor is a female mouth brooder ; adults more than 55 mm standard length are uncommon.

Distribution. Widespread in the lakes, rivers, swamps and streams of Uganda, and probably in other regions of eastern Africa as well. The species also occurs in the Nile.

DISCUSSION

Biology of the Lake George *Haplochromis* species flock

Detailed biological studies of the fishes are being carried out by members of the International Biological Programme team. Some of their results will be available shortly and it is thus appropriate now merely to make some general observations.

Unlike the Lake Victoria *Haplochromis* species, those of Lake George are less closely associated with a particular habitat or substrate type. Nevertheless, any one kind of habitat, for example, offshore open water, the papyrus fringe, protected bays or an exposed sandy shore, has a definable assemblage of species in which a few are numerically dominant.

Open offshore waters have the fewest species, and of these only a few are found also in other habitats, and then never as the dominant elements.

Species with clearly restricted habitat preferences are : the mollusc-eating *H. mylodon*, the supposed larval and embryo cichlid-eating *H. taurinus* and the grazer on epiphytic and epilithic algae, *H. limax*. Species caught infrequently (despite widespread sampling in many habitats) like *H. schubotzi*, *H. labiatus*, *H. nubilus*, *Hemihaplochromis multicolor* and *Astatoreochromis alluaudi*, may be presumed to have limited habitat preferences.

Only *Haplochromis petronius* can be said to have a truly restricted habitat since it is virtually confined to a rocky crater bay (the only one of its kind in the lake). Even in this example, however, there are exceptions since three specimens of *H. petronius* have been collected in the main lake (over sand and close inshore).

As with the *Haplochromis* species of Lake Victoria, the most readily observed adaptations seen in the Lake George fishes are those associated with feeding habits. Differences in tooth form and number, pharyngeal bone shape and dentition, and in jaw size and arrangement are the more obvious characters involved in this adaptive radiation. The overall impression gained is of a small-scale Victoria flock. In other words, one in which the major trophic adaptations are developed but to a slightly lower degree of specialization, and with fewer species occupying one trophic niche or showing the same level of specialization.

Lakes George and Edward harbour one trophic specialization not found among the *Haplochromis* of Lake Victoria, namely a species (*H. pappenheimi*) feeding, as an adult, almost exclusively on pelagic zooplankton. Possibly the absence of an *Engraulicypris* species from Lakes Edward and George has enabled a *Haplochromis* to fill this niche.

Two *Haplochromis* species in Lake Edward (*H. mylodon* and *H. pharyngalis*) have the enlarged pharyngeal bones and teeth associated with a diet of molluscs. Only *H. mylodon* occurs in Lake George, but, as in Lake Edward, another mollusc crushing cichlid, *Astatoreochromis alluaudi*, is present.

Specialized mollusc shellers (as opposed to crushers) have not evolved in the Edward–George flock. This specialization is well-represented in the *H. sauvagei–Macropleurodus bicolor* series of Lake Victoria (Greenwood 1957, 1965c). Possibly snails are a less abundant food source in Lakes Edward and George than in Lake Victoria ; qualitative sampling in all three lakes certainly suggests that this is so (personal observations).

Another sharp contrast between the flocks of Lake Victoria and George is the presence in Lake George of only one truly piscivorous species (*H. squamipinnis*). Among the inshore species of *Haplochromis* from Lake Victoria, about 30 per cent are piscivores. The situation in Lake Edward is different again because there are at least three piscivorous species among the known but yet undescribed species from that lake. However, the proportion of piscivores to non-piscivores in Edward is still much lower than in Victoria, probably about one in ten species.

A discrepancy is also noticed in the absolute number of larval and embryo fish-eating species. Only one paedophagus species, *H. taurinus*, is known from Lake George (and Edward) whereas at least seven species occur in Victoria. The relative proportion of paedophages to all other species (from all habitats and trophic groups) is, however, less disparate, being *ca* 6 per cent in Lake George and *ca* 4 per cent in Lake Victoria.

Although there is only one epiphytic and epilithic algal grazer in Lake George (*H. limax*) as compared with at least four such species in Lake Victoria (Greenwood

1956b), the total for Lakes Edward and George together is three, proportionately a much higher number than in Lake Victoria.

It is difficult to generalize about the insectivores and detritus feeders, except to say that in both flocks species belonging to these trophic groups are numerous (Greenwood 1965c).

At least one species in Lake Victoria (*H. erythrocephalus*) and one in Lakes Edward and George (*H. nigripinnis*) is a specialized feeder on suspended phytoplankton.

In Lake George there is a very rapid extinction of incident light so that over much of the lake the photic zone extends merely to a depth of about 60 cm. Most *Haplochromis* species live below this zone or at least spend a great deal of the day in very poorly lit waters. This raises several interesting questions regarding the fishes' adaptations and behavioural responses to such photic conditions. In particular there are problems associated with breeding behaviour ; there would seem to be insufficient light for potential mates to recognize one another visually. Another difficulty associated with breeding is the nature of the substrate in Lake George. Over much of the lake the bottom is composed of soft, near liquid, organic ooze. This would appear to provide a most unsuitable substrate on which to spawn in the typical *Haplochromis* fashion. There are, of course, places in the lake where the bottom is hard and where there is reasonably good light penetration. But, no evidence has been collected to suggest that these areas are the only ones used as spawning sites. Brooding females have been found in all habitats, although this does not necessarily imply that the spawning site was near by. It does, however, indicate that for the species involved there are no definite ' nursery ' zones.

Field conditions in Lake George virtually preclude direct observations on the fishes' spawning behaviour, and what information we may get in the future must therefore be indirect, i.e. from aquarium studies. A comparative study of the Lake George species with those from the deep, near-aphotic waters of Lake Victoria would be particularly valuable, especially since the latter species are also faced with a generally soft substrate.

Whether or not vision plays an important part in courtship and species recognition, the Lake George *Haplochromis* species, like those from other and clearer lakes, show distinctive and species-specific male coloration. The Lake George species do, however, differ in one respect. Many females have large, pigmented spots in the same position and of the same colour as the ocelli (or egg dummies, *see* Wickler 1962) in males. These pigment spots lack the clear border that, in males, makes the spot an ocellus. Unfortunately I do not know if female ' egg spots ' are so well developed, or if they are present at all, in Lake Edward populations of the same species.

As a footnote to these remarks on coloration it may be noted that no Lake George (or, as so far recorded, no Lake Edward) *Haplochromis* species exhibits a colour polymorphism like that found in several Lake Victoria species. In these fishes a certain percentage of females has an outstanding coloration in the form of piebald black on silver or black on yellow, or a peppered black, red and orange on a yellowish background. Sex-limited polychromatism is now recorded in at least eight species from Lake Victoria, but none has been found in any Lake George species from among the thousands of *Haplochromis* specimens examined by the I.B.P. team.

This absence of polychromatism in the Edward-George flock is rather surprising, not only in view of the flock's obvious relationship to that of Victoria, but because polychromatism is found in species of *Haplochromis* from Lake Kivu (*see* Poll 1939b). (The Kivu *Haplochromis* are related to those of Lake George in probably much the same way as are those of Lake Victoria.) No explanation is immediately apparent.

Species living in such poorly lit waters as those of Lake George might be expected to show certain compensatory hyperdevelopment of various sensory organs, especially the eyes and acustico-lateralis systems. Only the gross morphology of these organs has been investigated so far, and the conclusions reached are equivocal. The cephalic lateral line canals and their openings are not noticeably enlarged. In general, the eye (as measured by its diameter relative to head length) of Lake George species does not seem to be greatly enlarged. A comparison was made between the mean eye diameter in Lake George *Haplochromis* and their ecological counterpart species from Lake Victoria (the comparisons confined to individuals of the same size, and from species with the same maximum adult size). In the Lake Victoria species examined, the range of mean eye diameter is from 27·0–31·0 per cent of head length, whereas in the Lake George species it is from 28·0–38·0 per cent (the modal range being 31–35 per cent). *Haplochromis squamipinnis* is excluded from these figures because individuals attain a larger adult size, and eye diameter proportions generally show a strong negative allometry with body length. When a comparison is made between *H. squamipinnis* and similar-sized individuals of Lake Victoria piscivores, no noticeable difference was noted in eye size (mean eye diameter for *H. squamipinnis* 23·0 per cent of head, *cf.* 20·0–26·0 per cent for the Victoria species).

These comparisons were extended to include species from the deeper waters of Lake Victoria (*see* Greenwood & Gee 1969), where light values are probably similar to those found below the upper 30 cm of water in Lake George. The deep-water Victoria fishes have a range of eye diameter between 25·0 and 36·0 per cent of head length, with a modal value at about 31·0 per cent. This compares with values of 27·0–38·0 per cent (modal range 31·0–35·0 per cent) for the Lake George species, a suggestive similarity.

A comparison of the cephalic lateral line canals in these two species-groups was most inconclusive, mainly because of the difficulty in quantifying the characters involved.

The relationships and history of the Lake George *Haplochromis* species

From both zoogeographical and historical standpoints, the fishes of Lake George should be considered in conjunction with those of Lake Edward. The two lakes are now interconnected by the Kazinga Channel, they share many otherwise endemic cichlid species, and there is no evidence to suggest that Lake George has ever been in direct connection with any other major water body.

Regrettably, it was neither possible to effect a full revision of the Lake Edward *Haplochromis* species, nor was it feasible to collect in parts of the lake never previously sampled. There is no doubt that many species remain to be discovered in the deeper (i.e. western) parts of the lake (as, for example, was the case in the deep waters of Lake Victoria). The few recent collections made in Lake Edward (by Dr Dunn of the I.B.P. team), coupled with a brief re-examination of existing collections, show that there are definitely several undescribed species from inshore habitats.

Despite the drawback of having to exclude Lake Edward in detail, the material examined, together with that from Lake George enables one to reconsider currently held views on the origin of the Lake Edward–George *Haplochromis* species flock. Such reflection is very necessary, both in view of the more detailed geological and palaeontological knowledge now available (Greenwood 1959c ; Doornkamp & Temple 1966 ; Bishop 1969) and because of the rather different conclusions I have reached on the interrelationships of the Lake George and Lake Victoria *Haplochromis* species (themselves extensively revised since Trewavas' [1933] pioneer work on the Edward–George species).

That the *Haplochromis* species flocks of Lakes Victoria and Edward–George have a close phyletic as well as a phenetic relationship is beyond doubt. What has still to be determined is whether the Edward–George flock was derived directly from part of the Victoria species assemblage, or whether the two flocks evolved independently, but in parallel, from common ancestral species.

Trewavas (1933) believed that Lake Edward '...received its Cichlidae, or their not very remote ancestors, from Lake Victoria,...'. This concept has been basic to thinking on the subject ever since (Brooks 1951 ; Greenwood 1959c ; Temple 1969). Trewavas' views were influenced mainly by the overall similarity of the *Haplochromis* species in the two lakes, and by the fact that three otherwise endemic Victoria species were thought to be present in both lakes (*see below*). At the time of Trewavas' paper there was little geological evidence available to suggest either the nature or the duration of the route through which the faunal exchange might have taken place. The Rivers Katonga and Ruizi (now with a drainage via swamp divides into both the Victoria and Edward–George basins) suggested a possible passage way, particularly if, in earlier times, the swampy areas were readily passable. Later, Wayland's (1934) geological and palaeoclimatic hypotheses seemed to support the idea of an aquatic connection between the lake basins (Greenwood 1951, 1959c).

The ichthyological evidence once used in support of a Victoria–Edward (and George) interconnection will be reviewed first.

On Trewavas' reckoning there were six cichlid species shared between the lakes, viz. *Hemihaplochromis multicolor*, *Astatoreochromis alluaudi*, *Haplochromis nubilus*, *H. guiarti*, *H. macrops* and *H. ishmaeli*. Furthermore, every endemic *Haplochromis* species from Lake Edward–George was, in her opinion, closely related to a species from Lake Victoria (the endemic Edwardian monotypic genus *Schubotzia eduardianus* providing the only clear-cut exception [but *see above* p. 215]).

As noted earlier, the idea of a close overall relationship between the Victoria and Edward–George *Haplochromis* is still valid (and in many instances is reinforced by new information). I would find it difficult, however, to establish a direct phyletic relationship of an ancestor-descendant kind between each Edward–George species and its Victoria counterpart (the supposed *H. guiarti* of Lake Edward and *H. mylodon* excepted).

It is my opinion that *H. ishmaeli*, *H. guiarti* and *H. macrops* are not present in Lake Edward or Lake George. The fishes once identified as *H. ishmaeli* are now placed in a new taxon (*H. mylodon*, *see* p. 172) and the specimens thought to be *H. macrops* do not conform with the revised definition of that species (Greenwood 1960), nor are they conspecific with any other endemic Victoria species (*see below*). The status of the supposed *H. guiarti* from Lake Edward is difficult to determine without a full revision of the Lake Edward *Haplochromis* ; no similar species occurs in Lake George. For the moment I can only say that *H. guiarti* might be the sole example of an otherwise endemic Victoria species occurring in Lake Edward. The importance of determining the identity of Edward '*H. guiarti*' needs no further emphasis.

Two specimens identified by Boulenger (1914) as *H. macrops* were kindly lent to me by the Berlin Museum. A detailed morphometric and morphological study shows that both specimens differ from *H. macrops* (*see* Greenwood 1960) in dental and certain proportional characters. One specimen (a female 70 mm standard length) can be identified as a specimen of *H. nigripinnis*. The other (64 mm standard length, probably a female) is of *H. macropsoides* (*see above* p. 162). A third specimen (in the British Museum [Natural History], reg. no. 1933.2.23 : 397), identified by Trewavas (1933), has outer jaw teeth with markedly oblique major cusps, quite unlike the acute cusps of *H. macrops* (*see* Greenwood, *op. cit.*). This specimen also differs from *H. macrops* in several morphometric characters. In all these divergent characteristics, and especially in its dentition, the B.M. (N.H.) fish agrees closely with the type (and some paratypes) of *H. vicarius* Trewavas, a Lake Edward endemic (*see* Appendix I, p. 238, for a discussion on the status of this species).

Thus, all three Lake Edward fishes formerly identified as *H. macrops* are now referred to endemic Edward–George species.

The identity of Edward–George specimens previously identified as *H. ishmaeli* is discussed on p. 176. All the specimens are now included in a new and endemic species from Lakes Edward and George, *H. mylodon*. Anatomically, *H. mylodon* is very like *H. ishmaeli* and *H. pharyngomylus* of Lake Victoria. The main interspecific difference lies in the coloration of the adult males. In this respect, *H. mylodon* bears the same relationship to its Victoria counterparts as do certain endemic *Haplochromis* species of Lake Nabugabo to their counterparts in Lake Victoria (*see* Greenwood 1965b). It could, therefore, be argued that *H. mylodon* represents an instance of direct speciation from an *H. ishmaeli* or *H. pharyngomylus*-like ancestor that invaded the Edward basin at some time past.

Material collected by Worthington from Lake Edward and subsequently identified by Trewavas as *H. guiarti* is polyspecific. In fact, only a small part of it can be confused with *H. guiarti* as currently defined (*see* Greenwood 1962). Of the remaining specimens, one resembles *H. squamulatus* of Lake Victoria, and the others show characters of the *H. victorianus H. serranus* species complex in that lake. It must be stressed that none of these specimens is referable to its Lake Victoria counterpart. Preliminary work suggests that in Lake Edward there are, in addition to an *H. guiarti*-like species, two other piscivorous species endemic to Lake Edward.

On the basis of preserved material alone, it is difficult to separate the *H. guiarti*-like specimens from the true *H. guiarti*. When specimens are placed side by side, the Lake Edward fishes are distinguishable on the basis of their total morphology, especially head shape. The situation here is quite comparable with that existing between *H. mylodon* and *H. ishmaeli* (or *H. pharyngomylus*) but without the benefit of information on live male coloration.

Turning for the moment to the cichlid species which are definitely shared by the lakes. *Hemihaplochromis multicolor* has such a wide distribution in eastern Africa (including the Nile) that it is irrelevant to this discussion. Its absence from Lakes Edward and George would be of greater significance than its presence.

Haplochromis nubilus has a somewhat more restricted range and can definitely be categorized as a species of the Victoria drainage basin. *Astatoreochromis alluaudi* can also be categorized in this way. Both species, unlike other Victorian *Haplochromis* and related genera, are common in streams and rivers entering the lake, and both penetrate for some distance into papyrus swamps.

Taken in its entirety, the ichthyological evidence does not really seem to provide a strong argument in favour of a strictly Victorian derivation for the Edward–George cichlid species. In particular it does not support the idea of derivation from a developed, or partly developed *Haplochromis* species flock, an idea that I had previously espoused (Greenwood 1959c ; also Temple 1969).

The degree of anatomical differentiation between most known Edward–George species and their morphological counterparts in Lake Victoria is sufficiently well marked to suggest that one is observing the results of parallel evolution and not direct speciation in Edward–George from an already specialized invader species. Since both *Astatoreochromis alluaudi* and *Haplochromis nubilus* are relatively eurytopic, their presence in both lake basins could mean that they were components of the cichlid complex inhabiting the area prior to lake formation. Possibly, but less likely on ecological grounds, the two species could have gained access to Lake Edward–George via the Katonga–Mpanga River system.

The distribution of the extant non-cichlid fishes in the area contributes little of value to this discussion (*see* Greenwood 1959c). Only the occurrence of *Barbus altianalis* in both Victoria and Edward–George argues strongly for some past connection between the basins (as it does for a connection with Lake Kivu ; *see below*). Otherwise, the non-cichlid fishes of these lakes have little in common ; the number of endemic Victoria fishes contrasts with the depauperate but clearly Nilo-Albertine nature of the Edward–George non-cichlid species assemblage (Greenwood, *op. cit.*).

At this point brief mention should be made of Lake Kivu and its small *Haplochromis* flock. Historically, Lake Kivu was derived from a river that once flowed northwards into what is now the Edward–George basin. This river was dammed by the formation of the Bufumbiro volcanic chain, probably during the late Pleistocene. As the embryo Kivu gradually filled, it found a new outlet, now the Ruzizi, which drained into Lake Tanganyika. Rapids in the Ruzizi seem to block the passage of fishes (at least northwards) between Lake Kivu and Lake Tanganyika, although certain non-cichlids (e.g. *Barilius moorii* and *Barbus pellegrini*) are found in both lakes, perhaps as relicts of an earlier, unimpeded river connection.

The *Haplochromis* of Lake Kivu definitely show no relationships with those of Lake Tanganyika, but are distinctly of the Victoria–Edward type. There has been no recent revision of the Kivu *Haplochromis* species, and data on their live coloration are unavailable ; furthermore, an examination of the type series of two species (personal observations) strongly hints of more species than are currently recognized (Poll 1939a, b).

Comparing the Edward–George *Haplochromis* with the Kivu species, on a purely morphological basis, suggests that the Kivu fishes are quite distinct, although showing affinity with Lake Edward–George species (or, in one case, a Lake Victoria species).

Of the Kivu species I have studied in detail, *H. astatodon* Regan resembles *H. serridens* of Lake Edward, *H. graueri* Blgr. (at least, that is, one of the types) resembles fairly closely *H. schubotzi*, and *H. paucidens* Regan has the general orodental specializations of *H. labiatus* but in many features is more like members of the *H. crassilabris* species complex in Lake Victoria (*see* Greenwood 1965b). *Haplochromis vittatus* (Blgr.), too, shows most phenetic affinity with a Victoria species group (especially *H. gowersi*, a member of the '*prognathus*' group in that lake ; *see* Greenwood 1967) ; it does not closely resemble *H. squamipinnis* of Lakes Edward and George.

The remaining Kivu *Haplochromis* species (and those still undescribed) I feel less able to comment upon. *Haplochromis wittei* Poll and *H. schoutedeni* Poll could be related to either *H. elegans* or *H. aeneocolor* of Lake Edward–George, especially the former species, while *Haplochromis adolphifrederici* (Blgr.), if it is distinct from *H. graueri*, has superficial resemblances to *H. schubotzi* and *H. schubotziellus* of Edward and George.

As noted earlier (p. 230) sex-limited female polychromatism occurs in at least two Kivu species (*H. wittei* and *H. adolphifrederici*) but has not been recorded from any of the Edward–George species.

A detailed revisionary study of Lake Kivu *Haplochromis* species may throw more light on their phylogeny. This would be of great interest because the ancestors of these fishes could have been derived from the proto-George–Edward flock (before the Bufumbiro dam was formed) or could have evolved after that time, from ancestors living in the river before it was dammed. Since this river originated in the Ruanda Highlands it might well have been populated by different species from those in the westward flowing rivers of the Kenya Highlands which populated the embryo Lakes Victoria and Edward–George.

Modern geological studies on the Pleistocene sequence in Uganda also seem to support the idea of parallel evolution in the cichlid species flocks of the Victoria and Edward basins. (*See* summaries in Doornkamp & Temple 1966 ; Bishop 1969). Older ideas and temporal sequences based on Wayland's pluvial hypothesis (1934) are no longer tenable.

The formation of Lake Victoria is currently dated at about the later mid-Pleistocene, and is thought to be consequent upon the reversal and ponding-back of rivers that flowed across its present basin into the western Rift lake system (i.e. into a proto-Lake Edward–George and Albert). For a summary of the evidence, *see* particularly Doornkamp & Temple (1966).

River reversal was initiated by local uplift along a line nearer the western Rift than the developing Victoria basin. As a result of this uplift the formerly westward-flowing rivers drained both to the east and to the west, an anomalous situation still persisting. Extensive swamps developed over the watershed, and today these provide an effective barrier to fish dispersal along the rivers.

If one accepts the geological evidence, then one must conclude that a lake existed in the western Rift some time before Lake Victoria started to develop as a series of small lakes in the eastern sections of the reversed rivers. There is good palaeontological evidence for the existence of the western Rift lake or lakes from at least Kaiso Formation times (earlier Pleistocene) onwards (Greenwood 1959c). Essentially, this fossil record is one of non-cichlid fishes so it throws little direct light on the question of *Haplochromis* relationships.

Judging from the reconstructed topography of western Uganda in the earlier Pleistocene (Doornkamp & Temple, *op. cit.*) there was a steep escarpment bordering the eastern shoreline of proto-Lake Edward–George. It seems unlikely, therefore, that *Haplochromis* species could enter this western lake after the formation of Victoria. Furthermore, if the species that evolved in the developing Lake Victoria were as stenotopic (i.e. lacustrine) as are their present derivatives, it is highly improbable that they would spread along the inter-lake rivers (even assuming that such a passage was physically possible).

Thus the conclusion seems inevitable that, for all of their histories as lakes, Victoria and Edward–George have been effectively isolated from each other, and that Lake Edward–George is older than Lake Victoria. Since both basins were filled from the same river systems (the old east–west drainage) it is reasonable to assume that their initial fish colonizers were the same. In other words, their present-day *Haplochromis* species flocks were derived from common ancestral species, presumably of the generalized type now represented by *H. bloyeti* (*see* Greenwood 1971).

One Lake George species, *H. petronius* (*see* p. 209), does not fit this picture of a close phyletic relationship between the flocks of Lakes Victoria and Edward–George. Nor does it seem to be related to the *H. bloyeti* stock. As discussed in greater detail above (p. 213), *H. petronius* shows marked affinities with *H. wingatii*, a species known from the Nile and Lake Albert (Greenwood 1971). The characters relating these two species (and also *H. pharyngalis* of Lake Edward ; *see* p. 214) are not present in any Lake Victoria *Haplochromis* species. It is unlikely, too, that these characters are products of convergent evolution.

To me, the implication is that *H. petronius* was derived from a different lineage than that of the other species. It cannot, of course, be told if that lineage occurred in the Victoria basin but failed to survive there. Certainly there is no indication of *H. wingatii*-like species in any of the streams and rivers flowing into Lake Victoria today.

That related species appear to have persisted in Lake Albert and the Nile, and also in Lake George, suggests that the ancestor of *H. petronius* entered that lake from a source other than the old westward draining rivers. The nearest living relative of *H. wingatii* is probably *H. desfontainesi*, a species now restricted to North Africa (*see* Greenwood 1971). Perhaps the ancestor of *H. petronius* (and *H. pharyngalis*) was a northern rather than an east–west river species, that gained access to Lake Edward–George from the Nile before the lake was isolated from that river by the Semliki rapids (*see* Greenwood 1959c).

The distribution of *Haplochromis nubilus* and *Astatoreochromis alluaudi* in Lakes Victoria and Edward George, as well as in the small lakes lying between these basins (Trewavas 1933) suggests that the species are remnants of the original species complex inhabiting the old east–west river systems. Trewavas (*op. cit.*) interpreted the presence of *H. nubilus* and *A. alluaudi* in Lakes Nakavali, Kachira and Kijanebalola as possible evidence of the route through which the postulated Victoria to Edward faunal exchange took place. It now seems more likely that the species are fluviatile relicts in those lakes. The absence of other and more typically Lake Victoria or Lake Edward species from these small lakes puzzled Trewavas (*op. cit.*, p. 311). Probably the explanation is simply that these species or their immediate ancestors were never in that area.

Elsewhere I have argued (Greenwood 1965c) that the *Haplochromis* species flock in Lake Victoria represents the amalgamation of several smaller flocks, each evolved in isolation from a common ancestor or, later in the lake's history, a few common ancestral species. The isolation I envisaged was essentially one of small lakes lying within the area of what is now the basin of a single large lake. The present fauna of Lake Edward–George could be looked upon as another of these isolates but one which, because its basin retained its physical identity, has been given the status of a separate species flock. Phyletically speaking it is perhaps wrong to do so. Rather, one should refer to it as the Edward–George subflock.

As matters stand, there is insufficient knowledge of the physical and ecological factors involved in the processes of speciation and adaptive radiation within the Edward George subflock. Lake George has now been sufficiently well sampled for one to be almost certain that some species occurring in Lake Edward are absent from Lake George. Likewise it is clear that there are many more species in Lake Edward than are currently recorded. (Personal observations on recent collections from Lake Edward.) Collections from the Kazinga Channel show that its cichlid fauna is virtually identical with that of Lake George. That is, the Edward species not recorded from George are also absent from the Channel (*see* Appendix II). It seems, therefore, that the channel is at least partially a differential species filter between the lakes. The factors inhibiting occupation by certain species (and these do include some from Lake George) have not been discovered. This question is yet another whose solution will depend upon learning more about the ecology of the fishes, especially those from Lake Edward.

The unusually complete fossil record for the fishes of Lake Edward shows that throughout the Pleistocene, and well into the Holocene, the non-cichlid fishes were more diverse than at present (Greenwood 1959c). The genera *Lates* and *Synodontis*, now absent, were present until local Mesolithic times, and another present-day absentee, *Polypterus*, persisted into the early Holocene (de Heinzelin's level N.F.P.R. at Ishango is now dated at *ca* 8000–10 000 years B.P.).

Depauperization of this Nilo–Albertine fauna was sudden and of a relatively recent date (*see* Greenwood, *op. cit.*, p. 73). Localized vulcanicity polluting the water (especially of inflowing streams) may have been a major factor in this process. The differential adaptability of species to these altered conditions could account for the fact that some survived while others were wiped out.

If the arguments presented above on the origin of the Lake Edward–George cichlids are sound, then these fishes must have survived the environmental hiatus that exterminated several non-cichlid species. There is no evidence that the cichlids or their ancestors reinvaded the lake after the volcanic period, although the time elapsed could have been sufficient for the flock to evolve (*see* Greenwood 1965b).

Assuming that the Edward–George *Haplochromis* evolved from mid-Pleistocene fluviatile colonizers implies that speciation and adaptive radiation took place in the presence of such predators as *Lates* and *Hydrocynus*. Worthington's ideas on the inhibitory effects of *Lates* and *Hydrocynus* on these processes are well known and well argued over (*see* Fryer & Iles, 1972, for a comprehensive summary of various viewpoints in this discussion). The history of the Lake Edward–George *Haplochromis* species flock now seems to provide an even stronger counter-argument to the Worthington hypothesis than the one presented in my 1959c paper. There, I had assumed that the flock was derived from an at least partly differentiated one (at the species and adaptational levels) invading from Lake Victoria.

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APPENDIX I

The status of *Haplochromis vicarius* Trewavas, 1933

Poll (1939), synonymized *H. vicarius* with *H. eduardii* Regan, 1921 on the grounds that the large collection of specimens available to him bridged the morphological gap distinguishing the species. However, Poll seems only to have considered as specifically trenchant the posterior extent of the maxilla, and does not mention the dental characteristics of either taxon. My experience with various *Haplochromis* leads me to place little importance on the maxillary character, but considerable value on the form of the teeth.

The question raised by Poll's proposed synonymy is complicated by the fact that the type series for *H. vicarius* is very probably polyspecific. One specimen is labelled ' Holotype ' although no holotype was formally designated (Trewavas 1933). This fish and at least two paratypes have a distinctive cusp shape to the outer teeth of both jaws (*see* p. 171), a cusp type that does not occur in the teeth of *H. eduardii* holotype. Furthermore, I can find no reasons to believe that the tooth shape in *H. vicarius* holotype represents an extreme variant of the *H. eduardii* tooth-type (or vice versa).

Thus, I would suggest that *H. vicarius* is specifically distinct from *H. eduardii*. When the Lake Edward *Haplochromis* species are fully revised I suspect that other characters will be found to support this separation.

APPENDIX II

Kazinga Channel fishes

During May and June, 1972, collections were made at several places in the Kazinga Channel, particularly in the neighbourhood of Katungura (approximately the midpoint of the channel). Other regions sampled were near the Lake George end of the channel and at Mweya, near the opening into Lake Edward. Small-mesh gill nets and a purse seine were used, and sites near the shoreline and in midchannel were sampled.

A list of the species collected in the area around Katungura, with notes on the region of the channel in which they most frequently occur, and a subjective evaluation of their abundance, is given below.

Haplochromis elegans : common inshore, especially near reed beds ; also caught offshore, but is less abundant there.

H. aeneocolor : inshore near reeds ; not very abundant.
H. nigripinnis : only in midchannel ; rare.
H. oregosoma : inshore ; rare.
H. macropsoides : inshore and midchannel ; rare.
H. mylodon : inshore ; very rare.
H. angustifrons : mostly from midchannel where it is fairly abundant ; occurs inshore but is rare.
H. schubotzi : inshore ; rare.
H. schubotziellus : rare in midchannel, even rarer inshore.
H. taurinus : midchannel only and then infrequently.
H. pappenheimi : abundant everywhere, particularly inshore. Unlike catches of this species in Lake George, those from the channel contained large (110–130 mm standard length) and sexually active individuals of both sexes.
H. squamipinnis : ubiquitous, but in small numbers.
H. eduardianus : infrequently caught, and then only by dip-netting among the reeds.

Collections made near the Mweya landing were hampered by technical difficulties ; only gill nets, set inshore and in midchannel, were used and then on but one occasion. These yielded specimens of *H. elegans*, *H. aeneocolor*, *H. angustifrons*, *H. taurinus*, *H. pappenheimi* and *H. squamipinnis*, all in small numbers.

Because of inadequacies in the sampling methods used at Mweya landing, and since only one collection was made there, this list must be incomplete.

It is surprising that the well-sampled Katungura area did not produce any specimens of *Haplochromis limax*, *H. nubilus* or *Astatoreochromis alluaudi*. All three species were found in similar habitats in Lake George. There is, of course, a noticeable water flow in the channel, but this alone could hardly be the cause of these particular species' absence. More probably, their ' absence ' is a reflection of the sampling methods used (and the time available for sampling).

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A GUIDE TO THE IDENTIFICATION OF THE *HAPLOCHROMIS* SPECIES FROM LAKE GEORGE

A simple dichotomous key cannot be compiled for these fishes. Intraspecific variability is high and few species can be diagnosed on the basis of single characters. Thus, this ' key ' should be used as a general guide rather than as a means of identifying a taxon without recourse to other discriminating characters included in the full species descriptions. It is based on adult and subadult specimens.

Haplochromis labiatus is not included here because only one Lake George specimen is known. A specimen of *H. labiatus* would probably key out to *H. elegans*, but its dental characters (*see* p. 198) should prove diagnostic.

Morphometric characters are defined on p. 145. Unless otherwise specified, ' teeth ' refers to the outer row of teeth in both jaws.

The Lake George species[1]

Teeth spatulate, the upper half of each tooth strongly incurved (*see* text-fig. 37) ; lower jaw shorter than the upper . . . . **H. eduardianus**

Teeth bicuspid or unicuspid and caniniform, sometimes a mixture of both, and occasionally with some tricuspids intercalated ; lower jaw not shorter than upper . *A*

A Scales on the chest very small and deeply embedded (difficult to detect), especially when compared with those on the belly ; a small scaleless area immediately anterior to the first dorsal spine . . . . **H. petronius**

Scales on chest not deeply embedded, not disproportionately smaller than those on the belly, and readily visible ; no naked area at base of the first dorsal spine . *B*

B A vertical row of small scales extending onto the fin membrane along the basal part of many (if not all) dorsal and anal fin rays and spines. Lower jaw long (42–57, mode *ca* 50 per cent of head length, showing positive allometry) and oblique ; teeth usually unicuspid. Adults reach a large size (> 150 mm) . **H. squamipinnis**

No small scales extending onto the dorsal and anal fins. Adults rarely more than 115 mm long, modally *ca* 80 mm . . . . *C*

C Lower pharyngeal bone massive (*see* text-fig. 16), most of its teeth strong and molariform . . . . **H. mylodon**

Lower pharyngeal bone not massive, if molariform pharyngeal teeth present, few in number, small, confined to middle row . . . . *D*

D Teeth few in number (32–48, mean 36 in upper jaw), stout, deeply embedded in jaw tissue (difficult to see) and, although bicuspid, of characteristic shape (*see* text-fig. 25) ; gape of mouth manifestly large, lower jaw 43–56, mean 47 per cent of head ; dorsal profile of head concave. Adults reach a standard length of 140 mm **H. taurinus**

Teeth otherwise than above ; mean lower jaw length less than 45 per cent of head usually less than 40 per cent . . . . *E*

E Depth of body less than 35 per cent of standard length (mean = 31 per cent) ; modal number of gill rakers 10 or 11 (but as many as 13), the rakers slender . . . *F*

Depth of body usually more than 35 per cent of standard length ; modal number of gill rakers less than 10 (usually 8 or 9) . . . . *G*

F At least the posterior third of the premaxilla without teeth ; teeth small, flat and of a characteristic shape (*see* text-fig. 30), 28–38 (mean = 32) in upper jaw. Body colour uniformly silver in both sexes. Body fusiform, its depth 27–31 (mean = 30) per cent of standard length . . . . **H. pappenheimi**

[1] The two other *Haplochromis*-group species are identified as follows:
More than 3 (usually 4 or 5) anal spines: *Astatoreochromis alluaudi.*
Many scales of the lateral line series without pores: *Hemihaplochromis multicolor.*

Entire length of premaxilla toothed; teeth relatively slender (*see* text-fig. 9), 42–60 (mean = 50) in upper jaw. Males dark, females greyish-silver. Body depth 30–34 (mean = 32) per cent of standard length . . . . . ***H. oregosoma***

G Teeth in outer row of both jaws with an obliquely truncate cusp (*see* text-fig. 14), long and movably implanted; 4 or 5 (rarely 3) rows of inner teeth in the upper jaw . . . . ***H. limax***

Teeth otherwise than above, and only 2 or 3 inner rows (often only 1 row) . . . *H*

H Usually less than 40 teeth in the upper jaw (34–42, mean = 38); teeth bicuspid, most without a well-developed flange on the major cusp (*see* text-fig. 3, and *cf.* text-fig. 5). Upper jaw 28–34 (mean = 30) per cent of head (i.e. equal to or less than the eye diameter) . . . . ***H. elegans***

More than 40 teeth in the upper jaw (40–60, mean = 50) . . . . . . *I*

I Distinct and prominent midlateral dark band running from behind operculum onto the caudal fin; snout length 31–40 (mean = 33) per cent of head ***H. schubotziellus***

No distinct midlateral band (or, if a series of short midlateral streaks present, the last not extending onto caudal fin); snout length usually less than 30 per cent of head length . . . . *J*

J When fish is viewed laterally, the upper margin of the orbit is seen to be continuous with the dorsal profile, or the eye appears to extend above this line . . . . *K*

The upper margin of the orbit lies below the dorsal profile of the head . . . . *L*

K Dorsal head profile sloping smoothly (not obviously interrupted by prominent premaxillary pedicels). Preorbital depth 12–15 (mean = 14) per cent of head. Outline of toothed area on lower pharyngeal bone broader than long (*see* text-fig. 12). Caudal fin not distinctly maculate . . . . . ***H. macropsoides***

Slope of dorsal head profile interrupted by the prominent premaxillary pedicels. Preorbital depth 13–19 (mean = 17) per cent of head. Outline of toothed area on lower pharyngeal bone noticeably longer than broad (bone appears long and narrow, *see* text-fig. 19). Caudal fin very distinctly maculate . . ***H. angustifrons***

L Thickened and papillose area of tissue preceding first gill raker of first gill arch; pseudorakers between inner and outer row of gill rakers especially well developed and prominent. Snout length 31–40 (mean = 33·4) per cent of head . ***H. schubotzi***

No manifestly thickened and papillose area preceding first gill raker (or if tissue in that region slightly thickened, definitely not papillose); pseudorakers absent or poorly developed. Snout length usually less than 30 per cent of head . . . *M*

M Caudal fin with an almost rounded distal margin . . . . ***H. nubilus***

Caudal fin with truncate or weakly subtruncate distal margin. Two species, viz.:

(i) Most teeth with a well-developed flange on the major cusp (*see* text-fig. 5). Upper jaw 30–38 (mean 35) per cent of head. Eye diameter 28–35 (mean = 31·4) per cent of head. Lips slightly thickened. Nostril opening much larger than the anterior opening to the nasal lateral line canal. Intestine *ca* 1½ times total body length . . . . ***H. aeneocolor***

(ii) Few teeth with a flange on the major cusp (*see* text-fig. 7). Eye diameter 33–40 (mean = 36) per cent of head. Lips not noticeably thickened. Opening to nostril of equal size to that of nasal lateral line canal. Intestine long (*ca* 2–2½ times total body length) and much coiled . . . . . ***H. nigripinnis***

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PRELIMINARY NOTES ON THE ONTOGENY OF THE FRONTAL BODY WALL IN THE ADEONIDAE AND ADEONELLIDAE (BRYOZOA, CHEILOSTOMATA)

P. L. COOK

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BY

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Pp. 243–263 ; 3 *Plates*

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ABSTRACT

Specimens of species belonging to 6 genera of the nominal family 'Adeonidae' have been found to exhibit two distinct forms of development of the calcified frontal body wall and the associated apparatus concerned with protrusion of the lophophore. The first type, found for example in *Adeona*, is interpreted as umbonuloid; the second, found in *Adeonella*, is interpreted as cryptocystidean. Both ontogenetic processes are briefly described, and some of the genera previously ascribed to the Adeonidae are provisionally placed together in the family Adeonellidae.

INTRODUCTION

The development of the calcified frontal body wall in the Cheilostomata and its relationships with the apparatus for protrusion of the lophophore have been discussed recently by Cheetham (1968), by Banta (1970, 1971) and by Tavener Smith & Williams (1970). Banta particularly considered some phylogenetic inferences resulting from his observations, and clarified and correlated much previous work, especially that of Silén (e.g. 1942) and Harmer (e.g. 1902, 1957). Both Cheetham and Banta introduced methods and defined criteria which may be applied to future studies affecting the taxonomy and classification of the Cheilostomata (*see also* Boardman & Cheetham 1969, Boardman *et al.* 1970). The observations made here, principally on a few members of one group, the 'Adeonidae', emphasize the fundamental nature of the problems which may be recognized as a result of this type of examination, and the wide scope for further study which has arisen from the most preliminary analysis.

The protrusion of the introverted lophophore in Bryozoa is effected by the increase in internal coelomic pressure as a result of muscular contraction. In the Cheilostomata the type of calcification restricts the region available for muscular action to the area of the frontal body wall. In the Anasca, the frontal membrane is that part of the body wall delimiting the internal coleom frontally. Increase in internal pressure is accomplished by the contraction of the parietal muscles which are attached to the frontal membrane and extend to the basal or to the lateral walls. In the Cribrimorpha, the relationships are essentially the same, although the frontal membrane is variously overarched by a lattice of calcified spinous structures, leaving a space, the epistege, above it (*see* Banta 1970). In those Cheilostomata in which the frontal body wall is extensively calcified, two forms of apparatus for lophophore protrusion are known at present. In the first form, an anasciform frontal membrane and parietal muscles are present at an earlier ontogenetic stage than the calcification of the frontal body wall. In the second form, a sac-like proliferation of sub-opercular cells becomes attached to parietal muscles at a later stage than the primary calcification of the body wall. The correlation between the apparatus and the form and ontogeny of the calcification is not, however, a simple one. Much work remains to be done, including re-examination of specimens of the specific examples given by both Silén and by Harmer, as preliminary work has indicated that some of these may not, in fact, illustrate the relationships originally ascribed to them (*see* p. 260).

The genera considered here have usually been included in a single family, the Adeonidae (*see* Bassler, 1953 : G213 ; Harmer, 1957 : 788). With few exceptions they share an erect, branching bilaminar form of growth. They usually possess adventitious and vicarious avicularia, and have sexual polymorphs, those modified for brooding being of a distinct type. Most, but not all, possess a frontal pore, or complex of pores, here considered to be spiramina.

The family name Adeonidae was introduced by Jullien & Calvet (1903 : 53), as 'Adeonidae, J. Jullien, 1903'. Hincks (1887 : 150) had used the name several times (pp. 153, 155) in his discussion of Busk's family 'Adeoneae' (*see* Busk 1884 : 177), but had not introduced it formally as the name of a family. Both Hincks and Gregory (1893 : 241–244) made interesting observations on the heterogeneity of forms included in the family, especially noting the different types of development of the spiramina or frontal pores. Examination of species nominally classified within 6 genera of 'Adeonidae' showed that two major forms of development of the calcified frontal wall were present, and that two forms of protrusion apparatus could either be observed or inferred to be correlated with them. The genera have therefore been separated into two family groups, for convenience.

Adeonidae Jullien, 1903. Development of frontal wall umbonuloid (*see* p. 256). Operculum not sinuate. Marginal pores present. Frontal spiramina present, evanescent or permanent, single or multiporous. Avicularia with acute rostra usually present, adventitious and vicarious. Sexual polymorphs sometimes present, brooding internal.

Examples : *Adeona*, *Adeonellopsis*, *Reptadeonella*, *Bracebridgia*.

Adeonellidae Gregory, 1893. Development of frontal wall cryptocystidean (*see* p. 257). Primary calcified orifice and operculum sinuate. Marginal and usually frontal pores (pseudopores) present. Peristomial spiramina sometimes present.

Avicularia with acute and spathulate rostra usually present, adventitious and vicarious. Sexual polymorphs sometimes present, brooding internal.

Examples: *Adeonella, Laminopora.*

Many other genera, especially fossil examples, which have been placed in the 'Adeonidae', require investigation. Recently, some have been ascribed to other families (*see* p. 260 for summary).

Most of the specimens examined, from the collections of the British Museum (Natural History) (B.M.) and from the United States National Museum (U.S.N.M.) were in the dry state. Many very large, almost complete colonies in the British Museum were collected at least 90 years ago, and the growing edges were damaged and the surfaces covered with dirt. Detached pieces of these and whole specimens of the smaller colonies were soaked in 10 per cent trisodium phosphate solution for 24 hours, washed in water and gently cleaned in dilute detergent with a camel-hair brush, under a low-power microscope. This cleaned and restored much flexibility to the cuticular parts with little resulting damage. The specimens were examined in water after treatment, and differences in appearance noted when they were again dried. Similar comparisons were made between specimens preserved in alcohol and living colonies. Specimens of Adeonidae and Adeonellidae, together with some of species of Microporellidae, Inversiulidae and Umbonulidae, were also decalcified and sectioned. Some sections of *Reptadeonella* and *Escharoides* comprising soft and hard parts *in situ* were also examined. The ontogeny of frontal wall calcification has been directly observed in living specimens of *Reptadeonella.*

Specimens are referred to by the names and numbers under which they are currently stored. Many unnamed specimens of *Adeona* spp. at the British Museum (Natural History) together with MSS notebooks and drawings by Busk have been examined, but no attempt has been made to assign the material to described species, as a full study, particularly of the Australian reticulate forms, would first be necessary. Lack of suitable material has also restricted study of some forms; for example, it was found impossible to prepare specimens of *Bracebridgia pyriformis* (the type-species of *Bracebridgia*) to show the ontogeny satisfactorily.

Terms used. *Zooid* is used for a unit of the colony, *autozooid* for an individual inferred or observed to have a feeding function. The term *sexual polymorph* is used for zooids which differ from the majority of autozooids in their calcified parts, and which may also be observed or inferred to have a sexual function, in some cases demonstrably as male individuals, in others as female brooding zooids. Much further work is needed to establish the kind and degree of sexual polymorphism occurring in the Adeonidae and Adeonellidae. The term *brooding zooid* is here used for sexually polymorphic zooids, which are usually enlarged in a lateral direction, and which have been observed, or can be inferred to have contained embryos.

The term *lophophore* includes tentacles and supporting structures, e.g. the tentacle sheath; *ascus* refers to a sacciform structure derived from invagination of epidermal cells, and *ascopore* is restricted to a pore leading through both calcified and adjacent membranous layers into an ascus. The term '*epistegal space*' is used to denote the space above the frontal membrane in forms with umbonuloid development. It is analogous in function with an ascus, but developmentally similar in its relationships to a cribrimorph epistege (*see* Larwood 1962). The term *spiramen* is here restricted to a pore leading through calcified tissues and adjacent membranous layers to a space which is morphologically frontal in position to the operculum (*see* p. 257).

OBSERVATIONS ON THE ADEONIDAE

1. *Reptadeonella violacea* (Johnston). *See* Harmer, 1957 : 814.

MATERIAL EXAMINED. B.M., living (later preserved dry and in alcohol), Ghana, Vernon Bank off Tema, 10 m, collected 1968, 1970 and 1972, registered as 1970.2.8.19, 1970.8.2.12 and 1972.1.2.11, respectively. In alcohol, English Channel, 1966.1.10.104 ; dry, Brazil, 1888.4.16.14–17.

Zoarium encrusting. Autozooids with a simple frontal spiramen and a distally or distal-laterally directed suboral avicularium. Vicarious avicularia absent. Some sexual polymorphs present which are larger than autozooids, with a wider secondary calcified orifice ; these have been observed to contain embryos and are brooding zooids. Male zooid polymorphs not recognized.

Primary zooidal development consists of two major episodes of rapid ontogenetic change, separated by a period of apparent quiescence. The edge of colonies in active growth consists of a zone of uncalcified buds, covered by distended, pale yellow cuticle. The calcification of basal, lateral and distal walls is rapid, and separate zooidal units are observable after 6–8 hours. Peripheral series of 2–4 rows of partially calcified zooids remain in this condition in the laboratory, with little apparent change for as long as 14 days. Under normal conditions this quiescent period may well be shorter, but the great majority of well-preserved colonies in the British Museum shows a zone of partially calcified zooids at the growing edge, and thus some pause in the calcification process seems to be usual. Primary calcification of the frontal body wall is extremely rapid and may be complete in less than 12 hours. Calcification commences as a thin lamina which is an inward extension of the proximal and lateral walls. The lamina advances distally and medially beneath the cuticle leaving regularly spaced uncalcified areas. These become the marginal pores at a later stage. In the central area of the membranous frontal wall the parietal muscles and, distally, the operculum are differentiated at this stage. The central part of the membrane then becomes depressed (probably as a result of the contraction of the parietal muscles), and the advancing calcified lamina can be seen to continue its development above the membrane, forming the ' epistegal space '. The developing lophophore can be seen beneath the membrane at this stage.

The membranous frontal body wall thus assumes the same relationship with the developing lophophore and viscera as does the frontal membrane in Anascan species, and the overarching calcified frontal shield assumes the same relationship with the frontal membrane as does the spinous frontal shield in the Cribrimorpha.

As calcification proceeds the tissues underlying the cuticle become brightly pigmented. The purple colour is at first concentrated around and above the marginal pores ; it spreads and darkens in later ontogenetic stages, and remains under the distended cuticle, even when the calcified layers beneath it have reached considerable thickness.

As the calcified lamina extends distally and medially over the frontal membrane, it develops paired, medially directed distal processes which meet and fuse centrally above the now fully functional operculum (*cf.* Pl. 1, figs. 1, 2). Thus a secondary, calcified orifice is formed. This differs from that of the cryptocystidean orifice of, for example, *Watersipora*, in that it is not in direct contact with, and does not exactly outline, the operculum, which is slightly below it. In *Watersipora* the primary orifice is calcified and is formed as a result of the contemporaneous differentiation of the operculum and the calcification of the surrounding membranous frontal body wall (*see* Banta 1970). In *Reptadeonella* the primary orifice is uncalcified and is formed by the opening of the operculum. The central foramen formed by the median fusion of the distal calcified processes (*see* Pl. 1, fig. 2) becomes reduced in size by further, centrally directed calcification, but remains open as a frontal spiramen. It is visible, even in zooids with considerably thickened frontal calcification, as a pit, lined with pigmented tissue beneath distended cuticle.

The lophophore and viscera are completely formed before the fusion of the distal processes, and the tentacles have been seen to be partially protruded at this stage. Generally the autozooids are feeding actively while the avicularian chamber is being formed, soon after the formation of the secondary calcified orifice. Brooding zooids have not been seen to protrude tentacles, nor have specifically male zooids been recognized. Thus many details of the degree and nature of sexual polymorphism are at present lacking.

Subsequent ontogenetic changes, although continuous, are apparently far slower than these primary episodes, and consist mainly of the thickening of frontal wall calcification and the development of secondary adventitious avicularia.

All these ontogenetic changes may be inferred in well-preserved material by observing zooids at various stages progressively from the growing edge towards the ancestrular region (*see* Boardman *et al.* 1970). In specimens preserved in alcohol, the primary membranous frontal body wall, the developing calcified lamina, the operculum and parietal muscles and the fusion forming the secondary calcified orifice can all be seen, although the cuticle is not as distended as in life. In dried specimens the cuticle covering the calcified lamina is shrunken and not easily visible, but the frontal membrane and operculum can be seen beneath the developing calcified frontal shield in some zooids.

2. *Adeona* sp. (Pl. 1, figs. 1–6).

MATERIAL EXAMINED. B.M., dry, ? Australia, 1934.2.10.8, and Port Jackson, Australia, 1886.5.26.1–4.

Zoarium erect, bilaminar and regularly reticulate, with round or oval fenestrae. Autozooids with a simple frontal spiramen and a median distal or distal-laterally directed avicularium proximal to the secondary calcified orifice. Vicarious avicularia rare. Fenestral kenozooids regularly present. Some polymorphic zooids occurring in groups. These are large, with wider secondary calcified orifices than the autozooids, and are inferred to be brooding zooids ; separate male zooids not recognized.

At the growing edge there are zooids with basal lateral and distal calcified walls only, and with a shrunken membranous frontal wall. Proximally to these are autozooids with an incomplete curved calcified lamina, or a complete lamina, with a large central pore, beneath which the frontal membrane and operculum can be seen. Even more proximal zooids, at a later ontogenetic stage, show the development of the frontal avicularian chamber (*see* Pl. 1, figs. 4, 6). Scanning photographs show the distal median suture in the primary lamina, formed by the fusion of two distal lateral processes, as in *R. violacea* (*see* Pl. 1, fig. 3). They also show the progressive thickening of the calcified frontal shield, inferred from the increasing depth of smooth calcification lining the peristome, and the deepening of the pit formed around and above the frontal spiramen. The appearance of these specimens is very similar to that of dry specimens of *R. violacea*, and is inferred to represent a similar series of ontogenetic changes.

3. *Adeona foliacea* Lamouroux. *See* Harmer 1957 : 790.

MATERIAL EXAMINED. B.M., in alcohol and dry, Jedan, Aru Is., Siboga Stn. 273, 301A, 371A, 1972.10.1.2,1.

Zoarium erect, bilaminar, lobate, and articulated. Autozooids with a single frontal spiramen and a distal-laterally directed suboral avicularium. Vicarious avicularia frequent, marginal, little differentiated from the autozooids, with a frontal spiramen. Brooding zooids inferred to be the larger zooids of the lateral rows. Separate male zooids not recognized.

The earliest ontogenetic stages are not present, even in specimens preserved in alcohol. There are indications of a primary lamina in some broken zooids at the growing edge which suggests that the ontogeny resembled that of *Adeona* sp., above. The later stages, including the derivation of the median suboral avicularium chamber which is associated with paired lateral marginal pores, are the same as those seen in *Adeona* sp., above.

The large vicarious avicularia appear to develop in a similar manner to the autozooids, and have a frontal spiramen proximal to the rostrum. Unfortunately, none of the early stages in vicarious avicularian development has been preserved, and decalcified whole mounts show that there are no lophophores present in individuals at the later stages. Embryos have been seen in some of the submarginal zooids and these, at least, are therefore inferred to be brooding zooids.

4. *Adeonellopsis meandrina* (O'Donoghue & de Watteville) (Pl. 3, figs. 1–3). *See* O'Donoghue & de Watteville 1944 : 425, pl. 16, fig. 14.

MATERIAL EXAMINED. B.M., dry, Cape of Good Hope, 1840.9.30.29 ; Port Nolloth, South Africa, 1942.8.6.31 ; Lamberts Bay, South Africa, 1963.9.4.21 ; South Africa, 1968.1.16.125, 126.

Zoarium erect, bilaminar, foliaceous, convoluted and anastomosing. Autozooids with a simple frontal spiramen and paired medially directed lateral avicularia. Vicarious avicularia absent. Polymorphic zooids larger than autozooids, with wide secondary calcified orifices, inferred to be brooding zooids. Separate male zooids not recognized.

Stages in the development of the primary calcified lamina and frontal spiramen above the frontal membrane, like those in *R. violacea* and *Adeona* sp. above, have been seen. The development of the paired avicularia differs in that each chamber is derived separately from a marginal pore. In some zooids only one avicularium develops (*see* Pl. 3, fig. 3). Large polymorphic zooids are scattered in groups, and are inferred to be brooding zooids.

5. *Adeonellopsis* sp. (Pl. 2, figs. 1–3).

MATERIAL EXAMINED. B.M., dry, Broughton Island, Australia, 1883.11.29.55.

Zoarium (inferred from fragments) erect, with wide bilaminar, unbranched, crenulate and anastomosing laminae. Autozooids with a multiporous frontal spiramen, and a single median distal or distal-laterally directed avicularium. Vicarious avicularia large, scattered, directed distally. Brooding zooids inferred to be those larger than autozooids, with a larger multiporous frontal area.

The early ontogenetic stages in calcification of the primary lamina above the frontal membrane resemble those described above (*cf.* Pl. 1, fig. 4 with Pl. 2, fig. 1). After the fusion of the two processes in the distal part of the lamina, zooids at later stages differ in that the frontal spiramen calcifies as a large, porous plate. In the earliest stages finger-like processes protrude into the uncalcified central area. In later stages these fuse, forming a group of irregular pores. Further calcification consists of another series of processes which grow across the pores, producing a stellate effect. The smooth surface of the processes is similar to that of the calcification lining the peristome and the inner surface of the avicularian rostra. It contrasts strongly with the rounded blocks of calcification composing the frontal shield, as seen in frontal view (*see* Pl. 2, figs. 2, 3, and *see* Banta, 1971 : 168).

6. *Adeonellopsis* sp.

MATERIAL EXAMINED. U.S.N.M., dry, Australia.

Zoarium erect, bilaminar, branching. Autozooids with a single, stellate frontal spiramen and single or paired, distally directed suboral avicularia. Vicarious avicularia marginal. Sexual polymorphic zooids not recognized.

The earliest ontogenetic stages are rarely preserved, but appear to be similar to those of *A. yarraensis*, which this species strongly resembles. Use of the scanning electron microscope, however, has shown distinct differences in the mode of formation of the frontal spiramen. A pore is left as an uncalcified area as the frontal lamina grows distally, the calcification meeting distally beyond it. More proximally placed zooids show that as the frontal calcification thickens, the pore becomes sunken in a shallow pit, the sides of which are formed of smooth calcification. A series of finger-like processes grow medially from the sides of the pore, at its basal level, i.e. below the secondarily thickened surface level of the frontal shield. Zooids at this stage of development also show paired grooves apparently associated with lateral marginal pores, which protrude into the proximal edge of the secondary calcified orifice, their edges producing a small sinus. Later development of the grooves in a frontal direction produces the suboral avicularian chambers. The interior of the rostra is lined with smooth calcification, which also extends into the secondary calcified orifice, filling the sinus and forming a shallow, curved projection, similar to that seen in *Bracebridgia subsulcata* (*see below*).

7. *Adeonellopsis yarraensis* (Waters). *See* Harmer 1957 : 799.

MATERIAL EXAMINED. B.M., dry, Uraga Channel, off Tokyo, Japan, 30C, 1972.9.1.1.

Zoarium erect, bilaminar and branching. Autozooids with a multiporous frontal spiramen and paired distal medially directed suboral avicularia. Vicarious avicularia rare, marginal and small, directed distally. Large submarginal polymorphic zooids present, inferred to be brooding zooids.

At the growing edge, the development of the proximal part of the curved lamina above the frontal membrane can be seen. Zooids more proximal in position show that the later ontogeny differs from that described above for other species. The lamina continues to grow distally, but does not produce large paired processes which fuse. At the distal edge it leaves a series of small shallow depressions, each with a central slit. Four or five of these are formed and, at the same stage, two medially directed grooves develop leading from the nearest lateral oral marginal pores on each side. The next stage appears to comprise general thickening of the calcification, deepening the grooves which begin to form avicularian chambers. The frontal shield is also extended distally beyond the avicularian chambers and the last developed depression. Concurrently, the depressions, which have become sunken in the surrounding calcification, produce finger-like processes from their walls which grow centrally to produce stellate pores. As calcification proceeds, the whole complex appears to migrate proximally, but this is an illusion related to the thickening of the frontal wall. The base and sides of the depressions are formed of smooth calcification, like that lining the peristome and avicularian rostra, and unlike that of the surrounding frontal shield.

8. *Adeonellopsis* sp.

MATERIAL EXAMINED. U.S.N.M., dry, 'Albatross' Stn. 2324, Havana, Cuba, 33 fathoms, Stn. 2336, 23°10′ N, 82°18′ W, 157 fathoms. B.M., dry, Discovery Bay, Jamaica, 200 feet, 1965.8.2.3, Havana, Cuba, 80 fathoms, 1911.10.1.1274, as *Porina subsulcata*.

Zoarium erect, bilaminar, branching. Autozooids with a simple frontal spiramen, and a distally directed suboral avicularium. Vicarious avicularia marginal. Sexual polymorphs not recognized.

This species closely resembles the specimen of *Porina subsulcata* illustrated by Smitt (1873, pl. 6, fig. 136). It may be distinguished from *Bracebridgia subsulcata* (see below) by the constant presence of a simple frontal spiramen, by the distally directed, smaller suboral avicularium, and by the lack, in late ontogenetic stages of a raised ridge of calcification as in *B. subsulcata*. These closely similar species have been confused together, and the *Adeonellopsis* seems to be undescribed.

No zooids show the earliest stages of calcification ; but a few have a simple lamina overarching a depressed frontal membrane. Two zooids show the development of the frontal spiramen from a notch in the distally advancing lamina. Later ontogenetic stages indicate that the avicularium is associated with one of the lateral marginal pores. The distal part of the peristome is at first raised, but becomes immersed as the calcification of the frontal shield thickens. Later stages include the development of small, variously orientated adventitious avicularia on the frontal.

9. *Bracebridgia subsulcata* (Smitt). (Pl. 2, figs. 4-6.) *See* Smitt, 1873 : 28, pl. 6, figs. 136–140.

MATERIAL EXAMINED. Naturhistoriska Riksmuseet, Stockholm, dry, types of *Porina subsulcata* Smitt, Florida, 35 fathoms, Pourtales Coll., no. 1837 (for figs. 136, 137) and no. 1829 (for figs. 138–140). U.S.N.M., dry, 'Albatross' Stn. 2405, 28°45′ N, 85°02′ W, 30 fathoms. B.M., dry, 13°50′ S, 38°46′ W, 32-38 fathoms, 1890.1.30.17–20 ; 'Challenger' Stn. 122, off Bahia, 1887.12.9.735a, 1934.2.16.42, as *Adeonella distoma* var. *imperforata* Busk (1884 : 188, pl. 20, fig. 4).

Zoarium erect, bilaminar, branching. Autozooids with no obvious frontal spiramen, but with a distal-laterally directed suboral avicularium, its rostrum protruding above the proximal edge of the secondary calcified orifice, which also has a small rounded projection. Vicarious avicularia marginal. Sexual polymorphic zooids not recognized.

Very few growing tips show zooids at the earliest stages of calcification of the frontal shield. In two zooids only, distal processes of the lamina can be seen to have fused distally to form a small pore (Pl. 2, fig. 4). In one of these zooids the ridge delineating the proximal edge of the avicularian chamber has been formed, and the frontal spiramen, just proximal to it, is nearly occluded (Pl. 2, fig. 5). All other zooids inferred to have reached the same or later ontogenetic stages have no sign of a spiramen, which is presumably completely closed by the development of the avicularium and the thickening of the calcification of the frontal shield (*see* Pl. 2, fig. 6). The periphery of the shield develops as a raised, pyriform ridge of calcification, the central part of the shield remaining relatively depressed (*see* Pl. 2, fig. 6). In later ontogenetic stages further thickening obscures the ridge, and small, variously orientated adventitious avicularia develop on the frontal.

Smitt's fig. 136 shows zooids with distinct simple frontal foramina. His figured specimen indicates that these are a representation of the depression between the two lateral ridges of calcification in the later ontogenetic stages.

Adeonellopsis distoma (Busk), *see also* Busk (1884 : 187, text-figs. 56, 57), is apparently not closely related to *A. distoma* var. *imperforata*. *A. distoma* has an extensive multiporous frontal spiramen.

OBSERVATIONS ON THE ADEONELLIDAE

1. *Adeonella coralliformis* O'Donoghue (Pl. 3, figs. 4–6). *See* O'Donoghue, 1924: 55, pl. 4, fig. 24.

MATERIAL EXAMINED. B.M., dry, South Africa, 1923.7.26.15, 1962.6.4.13; dry and in alcohol, South Africa, 1963.3.20.21, 1968.1.18.5.

Zoarium erect, bilaminar, branching. Autozooids with frontal pseudopores and marginal pores. Primary calcified orifice with a distinct rounded sinus. Secondary orifice raised, with paired lateral avicularia directed distally and medially. A bar extends above the orifice extending from each lateral flange of the peristome, forming a small secondary calcified orifice distally and a peristomial spiramen proximally. Vicarious avicularia small, marginal, variously orientated. Enlarged marginal zooids inferred to be brooding zooids.

This species is very similar in several characters to *A. regularis* Busk (1884: 186, text-fig. 55, pl. 20, fig. 2), also from South Africa, and a study of the variation of the two forms is necessary.

The specimens are well preserved and the growing tips are intact. Zooids at the edge have basal, lateral and distal walls calcified, the frontal wall being entirely membranous. Other zooids in the same horizontal series, or slightly proximal in position, show development of a thin porous lamina of calcification beneath the membrane. In a few zooids the calcification is incomplete, but in the majority has reached the distal end of the zooid. At this stage the outline of the operculum and primary orifice within the central, rounded, uncalcified area is visible. The next proximal zooids have a fully formed primary calcified orifice and operculum. It is not possible to see the development of an ascus in whole decalcified mounts, but the appearance of the young zooids is very similar to those of *Watersipora*, *Fenestrulina* and *Onchoporella*, in which the rapid growth of the ascus as a sac developing from an invagination of subopercular epidermal cells can be seen. It is therefore inferred that the development in *Adeonella* consists of calcification of a cryptocyst beneath a hypostegal coelom and frontal wall of cuticle and epidermis, as described in *Watersipora* by Banta (1970), and in *Schizoporella* by Banta (1971).

Scanning electron microscope photographs show that the proximal part of the orifice calcifies in two stages (*cf.* Pl. 3, figs. 4 and 5). Concurrently, paired lateral oral avicularian chambers are developed, apparently associated with marginal pores, but often showing frontal pseudopores at the bases of their cavities. More proximal zooids show a general thickening of the frontal calcification and the growth of a raised lateral peristome, which incorporates the developing avicularian rostra. Paired processes then grow medially from each lateral peristomial flange, which meet and fuse, forming a bar beneath which the proximal part of the primary calcified orifice is visible. Later ontogenetic stages consist of general thickening of the calcification, immersing the peristome, and producing an apparent migration of the peristomial spiramen proximally. In decalcified sections the relationships of the spiramen and operculum are visible, the retracted tentacles extending to the area behind the operculum.

2. *Adeonella polystomella* Reuss. *See* Cook 1968a : 180.

Material examined. B.M., in alcohol, 5°24′15″ N, off Ghana, 1926.12.7.9 ; 'Calypso' Stn. 1, 27°05′ N, 17°14′ W, 45–43 m, C 51 I, C 52 D, 1970.8.21 and 8 ; Marche-Marchad Coll., Senegal, 1970.7.8.21.

Zoarium erect, bilaminar, branching and occasionally anastomosing. Autozooids with marginal pores and only one series of frontal pores, and a sinuate primary calcified orifice. Paired suboral avicularia very small, directed distally. Vicarious avicularia rare, small, distally directed. Sexual polymorphic zooids probably present.

The earliest ontogenetic stages have not been preserved, but near the growing tips a few zooids show a partially calcified, rounded primary orifice. More proximal zooids show the development of the sinus and operculum. Scanning photographs indicate that the primary orifice is calcified in two stages, as in *A. coralliformis*.

The frontal calcification differs from other species examined in the absence of pseudopores from the central area. Specimen 1970.8.21.1 includes the extensive, encrusting base of a young colony, and these zooids show a single submarginal series of pseudopores. The small oral avicularia appear to develop directly from a pair of lateral marginal pores. The marginal zooids are slightly larger than those in the centre and may be sexual polymorphs, but it is not known whether they are male zooids, brooding zooids, or both.

3. *Laminopora bimunita* (Hincks). *See* Harmer 1957 : 820.

Material examined. B.M., dry, Port Elizabeth, South Africa, 1899.5.1.1346 ; East London, South Africa, 1942.8.6.32 ; Durban, South Africa, 1968.1.16.6 ; in alcohol, False Bay, South Africa, 1962.6.4.11.

Zoarium erect, bilaminar, broadly foliaceous. Autozooids with frontal and marginal pores and a distinctly sinuate primary calcified orifice. Paired avicularia with long, acute mandibles, placed at the level of the sinus and directed proximally and medially. Large, distally directed vicarious avicularia rare and scattered, not marginal. Large sexual polymorphic zooids present, some inferred to be brooding zooids.

The specimens from False Bay show development of a porous calcified lamina beneath a thick primary membranous layer, presumably consisting of cuticle and underlying epidermis and coelomic tissue. The avicularia develop in association with marginal pores and concurrently with the formation of the primary calcified orifice. No peristomial spiramen is formed in any of these specimens, although it has been reported to occur in this species (*see* Harmer 1957 : 821). Later calcification greatly thickens the frontal wall, the primary orifices becoming sunken at the bottom of pits.

Large zooids with a wide sinuate primary orifice and relatively small avicularia are present in 1968.1.16.61, either marginal in position or scattered in small groups throughout the colony. It is not known whether some of these zooids are males, but, as Harmer described (1957 : 821), one type of large zooid has a narrow primary calcified orifice and sinus, the other, presumably the brooding zooid, has a wider primary calcified orifice with a shallow sinus.

4. *Laminopora contorta* Michelin, *see* Harmer 1957 : 819.

MATERIAL EXAMINED. B.M., dry, ? Cape St Vincent, 1854.11.15.334–336 (*see* Harmer 1957 *re* locality) ; in alcohol, 'Calypso' Coll. Stn. 14, 14°53′43″ N, 23°31′24″ W, 25–30 m, 1970.8.2, 10, Stn. 26, 15°16′30″ N, 23°47′31″ W, 50–65 m, 1970.8.2.6, Stn. 75, 16°04′20″ N, 22°58′10″ W, 45 m, 1970.8.2.5 ; Marche-Marchad Coll., Senegal, 1970.8.2.22.

Zoarium erect, bilaminar, irregularly branching, occasionally anastomosing. Autozooids with frontal and marginal pores and narrow, distinctly sinuate primary calcified orifices. Avicularia, if present, small, acute, lateral, directed distally. Vicarious avicularia rare, marginal, small, directed distally. Sexual polymorphic zooids marginal or scattered, slightly larger than autozooids.

The frontal calcification is similar in appearance to that of *L. bimunita*. Zooids with an incompletely calcified primary orifice, and with a porous lamina beneath a thick brownish-purple membrane, are inferred to indicate cryptocystidean development. The external cuticular membrane is distended in specimens preserved in alcohol. As the frontal calcification thickens, the primary orifice becomes sunken in a pit, as in *L. bimunita* ; in neither species is a distinct, tubular peristome produced like that in *Adeonella*. Decalcified sections show the introverted lophophore with its tentacles extending up to the operculum and completely filling the space behind it. Scattered large zooids have a wider primary calcified orifice than that of the autozooids and are frequently without avicularia. They are inferred to be brooding zooids, although in view of the possible bisexual nature of similar zooids in *L. bimunita*, further work is needed to ascertain their function.

DEVELOPMENT IN THE ADEONIDAE AND ADEONELLIDAE

The developmental series in the species assigned to the genera *Reptadeonella*, *Adeona*, *Adeonellopsis* and *Bracebridgia* have in common the growth of a calcified lamina above a frontal membrane, in which both the parietal muscles and the operculum are differentiated and functional early in the zooidal ontogeny. This type of growth is similar to that found in *Umbonula*, *Escharoides*, *Metrarabdotos* and in some features in *Exechonella*, and is termed 'umbonuloid' (*see* Cheetham 1968 : 58). Umbonuloid development has now been directly observed in living colonies of *Reptadeonella*, *Metrarabdotos* and *Exechonella*. In all three cases the early functioning of the parietal muscles, and their apparent contraction during development of the calcified frontal shield has been observed.

Umbonuloid growth may perhaps be regarded as the distal extension of a single layer of calcification from the gymnocyst above the frontal membrane. Theoretically this may be derived from a double-layered fold, in which the upper layer does not calcify. It is not known how nearly homologous this may be with some forms, at least, of Cribrimorph development, in which the gymnocystal extensions are spinous or derived from spines and must, therefore, be double-layered. Some supporting evidence is provided by study of living specimens of *Reptadeonella* and *Metrarabdotos*, both of which have strongly pigmented coelomic tissues. The cuticle in both forms is transparent and in life heavily pigmented tissue is present above the calcified frontal shield and beneath the distended frontal cuticle. This tissue is concentrated around the marginal pores and is present beneath the cuticle of uncalcified marginal buds. It is therefore presumably associated with coelomic tissues and is strongly suggestive of the presence of a coelomic connection at least, probably through the marginal pores (*see* Banta 1971). Nutritive coelomic tissue is thus present in umbonuloid forms beneath the cuticle but above the frontal calcified layer in a position which is analogous, but not homologous, with the hypostegal coelom of the cryptocystidean forms. The relationships of the calcified layer and the protrusion apparatus in the members of the Adeonidae studied are, however, exactly the same as that found in the Cribrimorpha, and the ' epistegal space ' above the frontal membrane is analogous and may be homologous with an epistege. Thin sections of Ghanaian specimens of *Reptadeonella* comprising both soft and hard parts *in situ* and sections of decalcified species of other umbonuloid genera (including *Umbonula*, *Escharoides* and *Metrarabdotos*) show that cuticle and cellular tissues are sometimes present lining the upper side of the epistegal space formed by the basal side of the calcified frontal shield. As cuticle and presumably coelomic tissues are present on the frontal side of the shield as well, the supposition that the shield represents a partially calcified fold is well worth further investigation.

Umbonuloid development differs from that described as ' gymnocystidean ' (*see* Banta 1970 : 53), in that the calcified frontal shield is an extension from the gymnocyst above a membrane, not an extension of the gymnocyst itself at the expense of the frontal membranous area. This last would lead hypothetically to the formation of an ascus by invagination of subopercular cells of epidermal origin as in the ' cryptocystidean ' type of development.

The formation of the frontal pore or pore-complex differs entirely from that seen in species of Microporellidae, which apparently have cryptocystidean ontogeny. In whole decalcified mounts of these forms the development of the ascus can be seen, and in sections the ascopore can be seen to lead directly into the ascus. The frontal pore in the Adeonidae leads into the space above the frontal membrane, and, as it is in a position morphologically above the operculum, is a spiramen. It is here defined as a frontal spiramen, to distinguish it from the peristomial spiramen of the Adeonellidae (*see below*). Although the frontal spiramen complex may be large, especially in some of the sexual polymorphs of *Adeonellopsis*, it is not yet known whether it is significantly involved in the passage of water into the ' epistegal space ', during protrusion of the lophophore. Thin sections of *Adeona* show that the spiramen does not become occluded by calcification during the thickening of the frontal shield. Observations have been made on living *Metrarabdotos*, which has no frontal spiramen, but an elongated narrow peristome comparable with that of *Reptadeonella*. Protrusion in *Metrarabdotos* was generally quicker and more frequent than in *Reptadeonella*, but in neither species was there any noticeable difference in behaviour between them and cryptocystidean forms with elongated peristomes, such as *Smittina remotorostrata* (Canu & Bassler), *see* Cook 1968a : pl. 8, fig. b, pl. 11, figs. c, d for general notes.

The later ontogenetic stages in the Adeonidae comprise the development of oral avicularia and the thickening of the frontal calcification. The single suboral, or paired, lateral-oral avicularia all appear to be derived in association with the marginal pores. Where the avicularium is single and median, as in many species of *Adeona* and *Adeonellopsis*, the chamber derives equally from both sides, a ridge forming suborally across the primary lamina distal to the frontal spiramen (*see* Pl. 1, fig. 4 ; Pl. 2, figs. 1 and 5). In *Bracebridgia*, only one lateral pore is involved. Concurrently, there is considerable thickening of the frontal calcification around the marginal pores and above the primary calcified lamina. The peristomial area also thickens frontally, although the peristome does not usually protrude above the general level of the frontal shield. In *Bracebridgia*, the distal part of the peristome is at first raised, but in later ontogenetic stages becomes immersed. The frontal spiramen becomes gradually obscured at the bottom of a pit in *Adeona* and *Adeonellopsis*, but in *Bracebridgia* is rapidly and completely occluded. In *Adeona* and *Adeonellopsis* in frontal view the position of the frontal spiramen appears to migrate proximally during ontogeny. Further calcification frequently occludes the frontal avicularia, and secondarily developed adventitious avicularia may be formed, with variable orientation, over the frontal shield.

There is evidence of a development series of increasing complexity in the ontogeny of the frontal spiramen, ranging from the single simple pore of *Adeonellopsis meandrina* to the multiporous complex of *A. yarraensis*. *Adeonellopsis* spp. nos. 5 and 6 above may show intermediate forms of development in the series, but further observations on other species are needed.

The developmental series in the species assigned to *Adeonella* and *Laminopora* is inferred to resemble that described as 'cryptocystidean' (*see* Banta 1970). The frontal calcification consists of a distally advancing layer, with marginal pores and frontal pseudopores, beneath membranous layers with presumably an intervening hypostegal coelom. No muscles or operculum are fully differentiated until the outline of the primary orifice has been formed by the calcification. Once the operculum has been formed, the ascus is developed by an invagination of subopercular cells and the parietal muscles presumably develop in succession proximally as the ascus enlarges (*see* Harmer 1902).

In *Adeonella* the peristomial area becomes extended and thickened distally and laterally, and raised lateral oral avicularia are frequently formed. The lateral peristome then produces medially directed extensions which meet and fuse in the midline, forming a peristomial bar above the primary orifice. Further lengthening of the peristome by frontal thickening of calcification produces a narrow secondary orifice and a long suboral peristomial spiramen, which, like the frontal spiramen in the Adeonidae, may appear to migrate proximally during ontogeny. A peristomial spiramen formed from fused lateral oral processes is known in several genera of Bryozoa, for example, in *Gigantopora* (*see* Harmer 1957 : 879).

Further calcification may obscure the first formed avicularia, and secondary, adventitious avicularia, variously orientated, may be produced, resulting in an appearance, in old, worn colonies, almost indistinguishable from specimens of *Adeona* at a similar ontogenetic stage.

Harmer (1957 : 805) considered that the 'ascopore' of *Adeona* and the 'spiramen' of *Adeonella* had fundamentally the same relationships. They both open into a space which is frontal in position in relation to the operculum, but differ entirely in structure, and in space and time relationships within the series of ontogenetic changes forming the calcified frontal body wall in the two families. Both types of spiramen differ from each other and from the ontogeny and relationships of the ascopore of the Microporellidae.

Banta (1970) has shown that conclusions drawn from examination of dried material, without comparison with well-preserved specimens showing the full ontogenetic series, are liable to be misleading. Where live specimens can be observed, and their appearance compared with those preserved in alcohol or as dry material, a sequence of inferences can be made with a fair degree of confidence. Banta has pointed out that the late ontogenetic stages in appearance of the cryptocystidean ascus and the umbonuloid equivalent are very similar.

Where a series of developing zooids is visible with a membrane which is left below the front of an advancing calcified lamina, and in which the operculum and parietal muscles are visible early in the ontogeny, umbonuloid development may be inferred. Comparison of stained whole mounts of growing edges of cryptocystidean species of *Watersipora*, *Stylopoma*, *Microporella* and *Onchoporella*, shows that the groups of cells producing the ascus take up stain differentially, and the developing ascus can be seen. This, together with other correlated observations, is taken to indicate cryptocystidean development.

In the absence of cuticle and epidermal layers, as for example in fossil material, it is at present impossible to do more than infer the course and type of calcification of the body wall by indirect means. Further investigations may provide more character correlations which will be recognizable in fossil specimens, and may lead to more confident inferences about their ontogeny (*see* Banta 1971 : 171). At present, for the Recent specimens studied, the following correlations may be suggested for those genera here assigned to the Adeonidae and to the Adeonellidae. Where members of a series of zooecia of increasing ontogenetic age can be inferred to develop a pore or pores in a primary lamina which has no pseudopores and which terminates in a non-sinuate, secondary, calcified orifice, and where the avicularian chamber or chambers are not associated with a raised lateral peristomial complex, the development is probably umbonuloid. Where members of a series of increasing ontogenetic age can be inferred to develop a porous lamina, terminating in a distinct, sinuate orifice and, in some cases, where a pore is produced by extensions from a raised peristomial avicularian complex, the development may be cryptocystidean.

DEVELOPMENT IN SOME OTHER FAMILIES

In the course of this investigation, specimens belonging to several other genera have been examined, notes made on the ontogenetic stages seen, and some types of development inferred. Within the 'Adeonidae', many fossil genera remain to be examined. For example, the genera *Schizostomella* and *Dimorphocella* possess individuals with sinuate orifices and apparent frontal spiramina, together with polymorphic zooids, which may be inferred, by analogy, to have had a sexual function. The characters of these genera are urgently in need of investigation.

Several Recent genera, some including fossil species, have already been revised, and the following notes summarize the current position. *Inversiula* was referred to the Inversiulidae by Harmer (1957 : 955), but replaced in the Adeonidae by Powell (1967 : 339), on the grounds that Vigneaux's prior definition (1949 : 68) of the family stated that gonoecia (brooding zooids) were absent and that therefore *Inversiula* was excluded. *Inversiula* appears to develop in a typically cryptocystidean manner, the ascus forming from an invagination of a group of cells concurrently with the differentiation of the proximal opercular margin. The plane of the closed operculum, which is hinged distally, is nearly vertical to that of the frontal wall, and the distal wall is very shallow. In decalcified sections, the ascopore can be seen to communicate directly with the ascus, and is completely separate from the operculum and region of the tentacle sheath, in the same manner as that seen in *Fenestrulina* and *Onchoporella*, both members of the Microporellidae. Although modified brooding zooids have been described in one species of *Inversiula* by Powell (1967 : 340), this would appear to be an interesting case of convergence with the Adeonidae and the Adeonellidae, and I consider that *Inversiula* has closest relationships with the Microporellidae.

Triporula (synonym *Enantiosula*) and *Anarthropora* were referred to the Exechonellidae by Cook (1967 : 965), and inferred to have modified umbonuloid development.

The genera *Trigonopora* and *Metrarabdotos* were referred to the Umbonulidae and the Metrarabdotosidae respectively by Cheetham (1968 : 59, 62), who considered them both to have umbonuloid growth. The living specimens of *Metrarabdotos* observed have confirmed Cheetham's conclusions. Other umbonuloid genera mentioned by Cheetham, none of which, however, have been referred in the past to the 'Adeonidae', were *Umbonula*, *Hippopleurifera*, *Hippomenella* and *Posterula*, all placed by him in the Umbonulidae, and *Exochella* and *Escharoides* which he referred to the Exochellidae.

Some genera referred by Harmer (1957 : 651) to the Ascophora Imperfecta, and thus inferred by later workers to have umbonuloid development, do not appear to display this type of ontogeny of the frontal wall. Some preliminary observations on members of the Petraliidae, Petraliellidae and Celleporariidae indicate that their development is not umbonuloid, but may be similar to the cryptocystidean type.

CONCLUSIONS

At present there are alternative conclusions as to the composition and relationships of the families Adeonidae and Adeonellidae. First, the similarity in colonial structure and polymorphism may be considered to be such that the ontogeny of the frontal shield and protrusion apparatus is not of phylogenetic significance. Second, it may be concluded that the groups are polyphyletic, exhibiting convergence between two or perhaps among several lines of evolution, and parallel development within these lines to a remarkable degree. I regard the testing of the second conclusion as that potentially the more fruitful for future investigations of the Cheilostomata in general. The necessary studies would involve Bryozoan workers in many fields for their completion, and observations on the following subjects would have to be made.

The form of the colony is preponderantly erect and bilaminar, but encrusting forms are known. The erect habit, with its positional dimorphism of central and marginal zooids and polymorphs, is known in several other groups, but has been insufficiently investigated. A study of these and of the early astogenetic stages may provide hitherto unrecognized patterns of colonial structure and evolution in many genera.

The occurrence of sexual polymorphs, both male and female, also with positional significance, was described and summarized for the 'Adeonidae' by Harmer (1957 : 788–821). It is also known in *Hippoporidra* (*see* Cook 1968b), and almost certainly occurs in other forms. Sexual polymorphs have probably not been recognized because the polymorphism is not necessarily reflected in the calcified parts of the individuals (*see also Hippopodinella* described by Gordon 1968), and the study of living specimens and of the lophophore and viscera has been neglected. Although sexual polymorphs have been observed and inferred in the Adeonidae and Adeonellidae, much more work, on living and preserved specimens, is needed to ascertain their detailed morphology and distribution. Preliminary examination of many fossil and Recent species has indicated that there are probably trends in the degree of differentiation of sexual polymorphs with time, which may have taxonomic and phylogenetic significance. The zooids inferred to be brooding zooids appear to be very similar in some representatives of the two families, but have not been certainly recognized in all genera. Similar kinds and degrees of polymorphism are known in other, obviously unrelated, genera, and a thorough investigation may throw light on the kind and degree of convergence which may have occurred in the Adeonidae and Adeonellidae.

Avicularia are almost invariably found throughout the two families and where present are consistently without a calcified bar. The vicarious avicularia vary from a relatively undifferentiated type, often with a frontal spiramen, to more complex individuals. Further work on their morphology and distribution, and comparison with similar types, particularly among the Anasca, would be instructive.

Electron microscopy will probably reveal considerably more evidence as to the structure and development of the calcified parts of Bryozoan colonies. It is most important that these observations are made in conjunction with those possible with a light microscope, in order that correlations may be made available for workers in the more conventional fields.

Taxonomic revisions, involving comparison of type-material with plentiful, well-preserved specimens, together with studies on population variation are urgently required, before any conclusions may be drawn as to the distribution of genera in time and space. Finally, after extensive work on fossil and Recent populations, it may be possible to construct a hypothetical phylogenetic model for the evaluation of the evolution of the Adeonidae and Adeonellidae, and to relate them to each other and, by extrapolation, to other Cheilostome groups.

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PLATE I

Adeona sp. ? Australia, 1934.2.10.8, Busk Coll.

FIG. 1. Zooecium from near growing edge; showing proximal and lateral frontal lamina, marginal pores and distal communication pores.

FIG. 2. Zooecium at a later ontogenetic stage; showing fusion of distal parts of lateral laminae forming median suture, formation of secondary calcified orifice and frontal spiramen. Note early stages in formation of avicularian chamber on either side of median suture.

FIG. 3. Same zooecium as fig. 2; showing suture.

FIG. 4. Zooecium at a later ontogenetic stage; showing frontal, upward extension of peristome after thickening of frontal shield, and development of avicularian chamber.

FIG. 5. Zooecium at a later ontogenetic stage; showing formation of single avicularium proximal to secondary calcified orifice; note apparent proximal migration of frontal spiramen.

FIG. 6. Zooecium at a later ontogenetic stage; showing formation of avicularian rostrum and condyles.

All photographs taken using electron scanning microscope.

Magnification: Figs. 1–2, 4–6, × 145; fig. 3, × 370.

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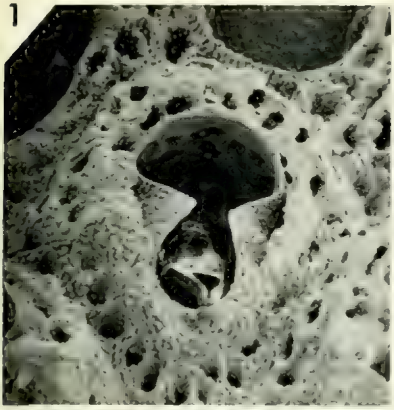

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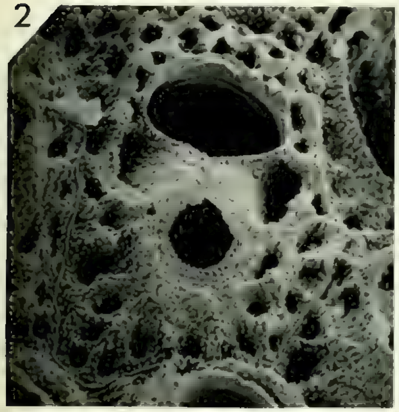

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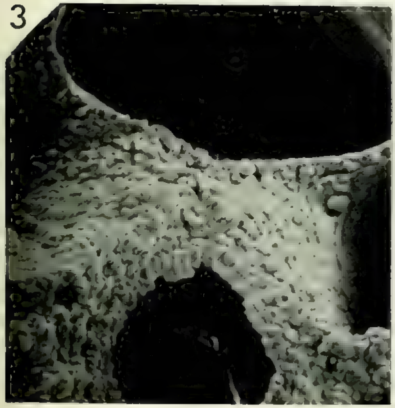

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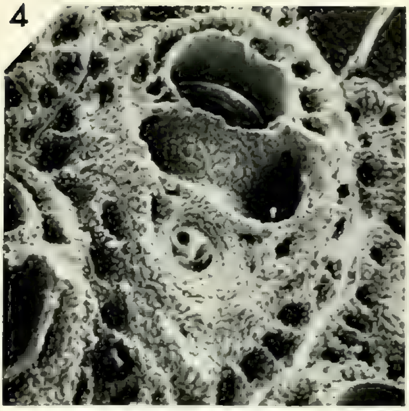

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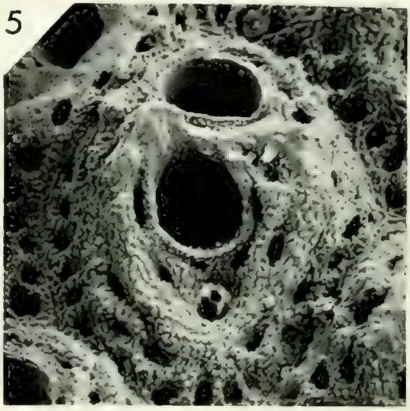

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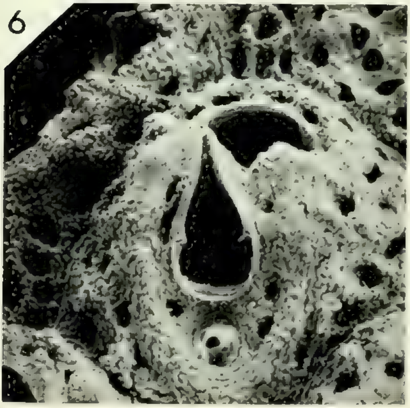

PLATE 2

Adeonellopsis and *Bracebridgia*

FIGS. 1–3. *Adeonellopsis* sp., Broughton Island, Australia, 1883.11.29.55.

FIG. 1. Zooecium near growing edge, showing primary lamina and secondary calcified orifice. Note the beginning of formation of suboral avicularian chamber and subdivision of central spiramen area into multiporous plate.

FIG. 2. Same zooecium; showing arrangement of blocks of calcification round the depressed frontal area.

FIG. 3. Same zooecium; showing frontal spiramen. Note the smooth calcification lining the pores.

FIGS. 4–6. *Bracebridgia subsulcata* (Smitt), 28°45′ N, 85°02′ W, 30 fathoms, 'Albatross' Stn. 2405.

FIG. 4. Zooecium near growing edge, showing primary lamina and frontal spiramen. Note that frontal, upward extension of peristome has already taken place, and suboral avicularian chamber has begun to develop.

FIG. 5. Zooecium at a later ontogenetic stage; showing partially occluded frontal spiramen and formation of avicularian chamber.

FIG. 6. Zooecium at much later stage; showing frontal suboral avicularium and calcification of proximal oral process; the peripheral ridge of frontal calcification is formed.

All photographs taken using electron scanning microscope.

Magnification: Fig. 1, × 120; fig. 2, × 300; fig. 3, × 600; figs. 4–6, × 140.

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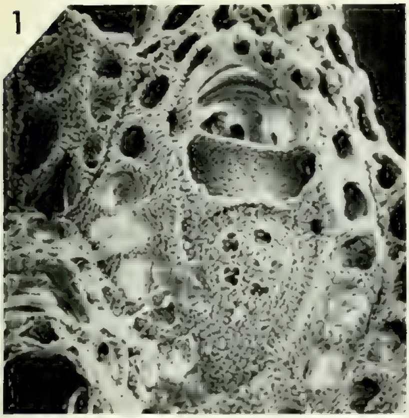

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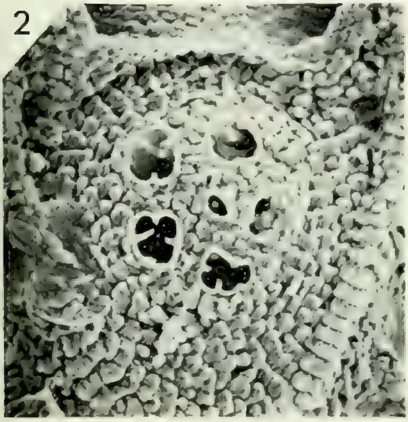

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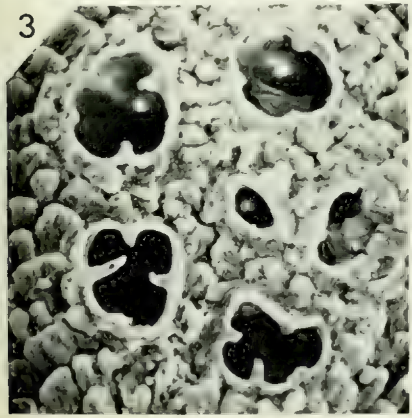

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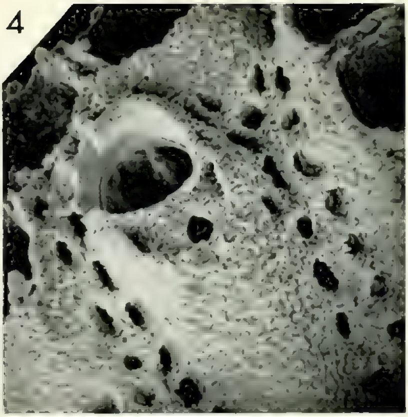

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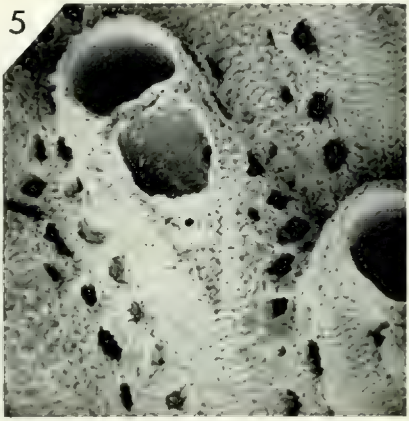

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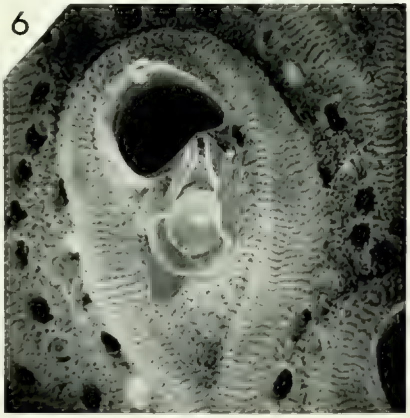

PLATE 3

Adeonellopsis and *Adeonella*

FIGS. 1–3. *Adeonellopsis meandrina* (O'Donoghue & de Watteville), Cape of Good Hope, 1840.9.30.29, Krauss Coll.

FIG. 1. Zooecium near growing edge ; showing frontal lamina at an earlier ontogenetic stage than that shown in *Adeona*, Pl. 1, fig. 1.

FIG. 2. Zooecium at a later ontogenetic stage ; showing formation of frontal spiramen and secondary calcified orifice.

FIG. 3. Zooecium at a later ontogenetic stage ; showing development of one of the avicularian chambers (frequently paired in this species).

FIGS. 4–6. *Adeonella coralliformis* O'Donoghue, South Africa, 1968.1.18.5, O'Donoghue Coll.

FIG. 4. Zooecium near growing edge ; showing early form of primary calcified orifice, frontal pseudopores and the early formation of avicularian chambers.

FIG. 5. Zooecium at a later ontogenetic stage ; showing fully formed primary calcified orifice, with complete sinus, further development of avicularian chambers, and early development of medially directed lateral peristomial processes. Note frontal, upward extension of peristome as frontal shield calcification thickens.

FIG. 6. Zooecium at a later ontogenetic stage ; showing sinus of primary orifice, complete avicularian rostra, formation of supraoral bar from fusion of lateral processes, and subsequent formation of secondary calcified orifice and peristomial spiramen. Note apparent proximal migration of peristomial spiramen.

All photographs taken using electron scanning microscope.

Magnification : Figs. 1–3, × 120 ; figs. 4–6, × 85.

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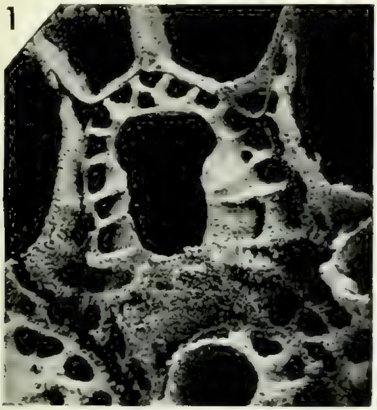

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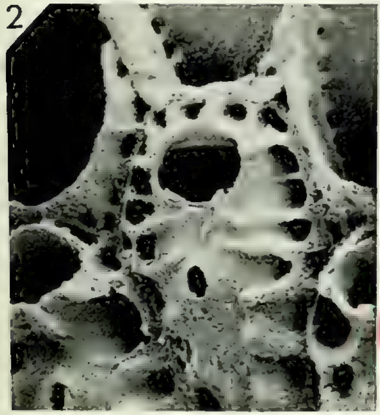

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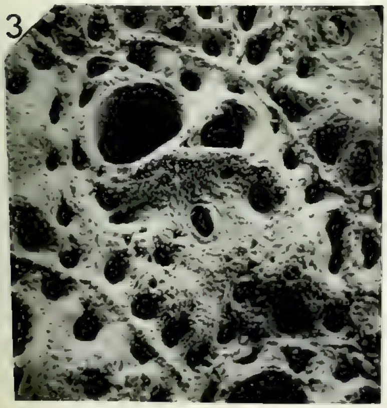

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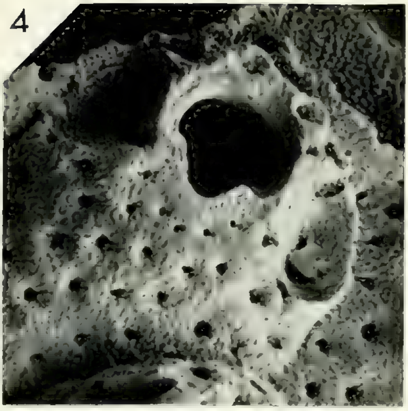

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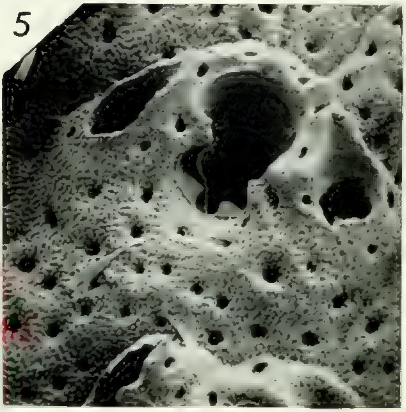

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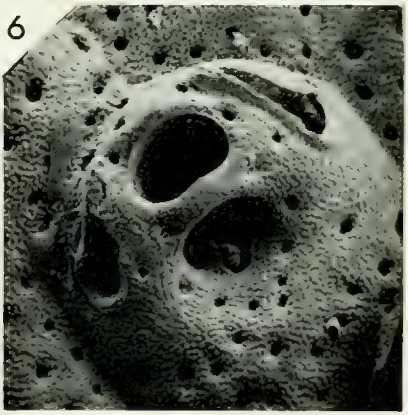

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SOME NEW TAXA OF RECENT STALKED CRINOIDEA

A. M. CLARK

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ZOOLOGY Vol. 25 No. 7
LONDON: 1973

SOME NEW TAXA OF RECENT STALKED CRINOIDEA

BY

AILSA McGOWN CLARK

Pp 265–288 ; 2 *Plates*, 6 *Text-figures*

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ZOOLOGY Vol. 25 No. 7
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SOME NEW TAXA OF RECENT STALKED CRINOIDEA

By AILSA McGOWN CLARK

SYNOPSIS

Two small families of present-day stalked crinoids are reviewed. The Hyocrinidae is divided into two subfamilies, one including a new genus from the North Atlantic. Another new genus from the same area is added to the Phrynocrinidae, from which the genera *Porphyrocrinus*, with a new species from the southern Indian Ocean, and *Naumachocrinus* are split off as a new family. The range of the bathycrinid *Democrinus chuni* is extended. New diagnoses are given for the four families mentioned and illustrations of the holotypes of two previously known species.

THE small remnant of the class Crinoidea surviving to the present day consists primarily of the free-living Comatulida or feather stars, leaving only about seventy recognized species of stalked sea-lilies. Nearly half of this total is made up by the handsome Isocrinidae, well known for more than 200 years despite their absence from shallow water and distinguished by their relatively large size, with stalks often more than half a metre long bearing whorls of jointed cirri. The present paper is, however, concerned mainly with two of the lesser-known four remaining families – the Phrynocrinidae with four species and the Hyocrinidae with seven. Recent collecting by the National Institute of Oceanography in the North Atlantic has yielded two new genera, one belonging to each of these families and has prompted a review of the included taxa.

I am indebted to Mr B. Rowbury of N.I.O. and also to Professor J. H. Day of the University of Cape Town, from whom came a third new species, this time from an un-named sea mount in the southern Indian Ocean.

Family **HYOCRINIDAE** P. H. Carpenter

Hyocrinidae P. H. Carpenter, 1884 : 217–218 ; Koehler & Bather, 1902 : 78 ; Koehler, 1909 : 264 ; A. H. Clark, 1912 : 272 ; Gislén, 1939 : 7–17.

In his review of this family, Gislén (1939) listed a number of differences between *Calamocrinus* Agassiz, 1890 and the remaining genera included, namely the presence of five basal plates, a marked angle between the basal and radial rings, arms almost as stout as the radials and branching several times, the brachials short and broad, the distal syzygies separated by more or less numerous muscular joints, the proximal pinnules only about a fifth as long as the arms, the tegmen (or disc) relatively high, extending to about the tenth post-radial ossicle, and the orals relatively small.

The angle in the calyx between basal and radial rings appears slight in Agassiz's drawings of the syntypes of *Calamocrinus diomedae* (Agassiz, 1892, pls. 2 and 3) though well marked in the additional specimen drawn by Westergren (in Agassiz's pl. 28). A new member of the family described below, closely related to *Hyocrinus*, does have a distinct angle between the two rings, at least in the anterior part of the calyx, and I do not think that this character is very significant. Some of the other differences, such as the relative stoutness of the arms of *Calamocrinus* in comparison with the radials and the shortness of the brachials, are likely to be correlated with the large size of the type material, calyx height *c.* 12 mm, whereas most of the other hyocrinids known do not exceed 8 mm calyx height. The relative shortness of the proximal pinnules, I think, is correlated with the fact that the arms branch. However, the presence of five basal plates (presumably primitive), the relatively small oral plates, the numerous muscular joints in the arms in comparison with the number of syzygies and possibly the fact of the arms branching and the very large size of the tegmen I consider are characters of supra-generic weight. Accordingly I am proposing a separate subfamily for *Calamocrinus*.

Diagnosis of family Hyocrinidae. A family of Articulata with a rounded stalk, sometimes slightly polygonal proximally with small tubercles in vertical series, without cirri, numerous proximal columnals discoidal and inflexibly jointed by synostoses in adults, increasing in number by intercalation between several segments, not just above the topmost one, attached to the substrate by an expanded terminal plate (when the attachment is known) ; the calyx with thin-walled plates, the sutures between the two rings and between the radials distinct, the three (rarely five) between the basals indistinct or lost by fusion ; the arms (or division series) abruptly narrower than the radials in adults, well separated laterally exposing the prominent tegmen (or disc), usually five simple arms (irregular branching normally in only one genus), syzygies usually alternating with muscular joints (except in *Calamocrinus* where syzygies are fewer and *Hyocrinus* where they are more numerous) ; only P_1 and P_a undeveloped, the proximal pinnules very long, with gonads lined by large side plates and with distinct cover plates running the whole length of the ambulacra ; oral plates usually enlarged.

Subfamily **CALAMOCRININAE** nov.

Diagnosis. A subfamily of Hyocrinidae with the basal ring made up of five similar plates ; arms branching several times irregularly, the first axillary not usually before the tenth post-radial ossicle ; muscular articulations considerably outnumbering the syzygies ; tegmen (or disc) very large, reaching up to about the tenth post-radial ossicle in adults ; oral plates inconspicuous.

Included genera. *Calamocrinus* A. Agassiz, 1890, type-species *C. diomedae* A. Agassiz, 1890 ; monotypic.

Subfamily **HYOCRININAE**

Diagnosis. A subfamily of Hyocrinidae with the basal ring made up of either a single fused ossicle or of three unequal plates (the sutures more or less indistinct) ; the arms normally unbranched ; the syzygies alternating regularly with muscular joints, with a few exceptions proximally where two successive muscular joints may occur; the oral plates much enlarged, forming a conspicuous cone in the centre of the disc, which is of moderate height, not usually extending beyond about the fifth brachial.

Included genera. *Hyocrinus* Wyville-Thomson, 1876, type-species *H. bethellianus* Wyville Thomson, 1876; monotypic.

Gephyrocrinus Koehler & Bather, 1902, type-species *G. grimaldii* Koehler & Bather, 1902; monotypic.

Ptilocrinus A. H. Clark, 1907, type-species *P. pinnatus* A. H. Clark, 1907; also including *P. antarcticus* Bather, 1908 and *P. brucei* Vaney, 1939.

Thalassocrinus A. H. Clark, 1911, type-species *T. pontifer* A. H. Clark, 1911; monotypic.

The following new genus is now added:

ANACHALYPSICRINUS [*] gen. nov.

Diagnosis. A genus of Hyocrininae with the more proximal stalk segments at least all discoidal in adult specimens, those immediately below the calyx tending to alternate in thickness and projection, with thicker and slightly tubercular-edged plates alternating with thinner intercalary ones; [the distal part of the stalk and its attachment unknown]; the calyx distinctly asymmetrical in adults owing to a marked inclination backwards (i.e. towards the CD interradius containing the anal cone) of the anterior half of the radial ring, although the basal ring is more evenly inverted-conical; three faint inter-basal sutures just distinct; arms unbranched, arising almost vertically from the calyx, only Br_3 with a muscular joint at both ends, elsewhere such joints alternating with syzygies, the brachial formula, $1 + 2, 3, 4 + \overline{5}, 6 + \underline{7}, 8 + \overline{9}$, etc., the first pinnule, P_2, being on the left side of Br_5 in each case.

Type-species. *Anachalypsicrinus nefertiti* sp. nov.

Affinities. These are discussed after the description of the type-species.

Anachalypsicrinus nefertiti sp. nov.

(Figs. 1a–e, 2. Pl. 1)

Material. 'Discovery' Investigations st. 7711/66; 53°11·2′ N : 20°5·1′ W–53°11·6′ N : 20°3·9′ W (North Atlantic, *c.* 400 nautical miles west from Northern Ireland), 2432–2380 metres. Holotype [B.M. reg. no. 1972.12.5.1] and three paratypes.

Diagnosis. As for the genus.

Description. The holotype (Pl. 1 fig. a) is the largest specimen and has the total height of calyx and disc 35 mm, much larger than any hyocrinid previously recorded. Numerical data from it are given in Table 1 with that from the two normal paratypes (the third being badly deformed).

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[*] Discovery-lily, from the collecting vessel.

Table 1

Some numerical data from the holotype (1) and two normal paratypes of *Anachalypsicrinus nefertiti* sp. nov. Measurements are in millimetres ; larger parts of the first two specimens were measured with calipers and the naked eye ; the rest with a micrometer eyepiece. The arm measurements are from the anterior arm in each case.

	1	2	3
Stalk :			
Length remaining	25	30	22
Number of segments remaining	50	68	76
Number of segments in top 20 mm	43	52	74
Diameter (below flared top)	3·8	3·6	1·1
Calyx :			
Diameter of lower end of basals	~5·0	5·0	1·7
Diameter of top of basals	14	14	3·6
Diameter (maximum) of radials	22	19+	4·4
Diameter (maximum) of one radial	13	11·5	2·6
Height of basals	10	9	2·5
Height of radials	15	12	3·3
Total height (including disc)	35	27	7·5
Post-radial series :			
Arm length	170	126	22
Breadth at 4 + 5	3·2	3·1	0·8
Length Br_1 to 4 + 5	4·0	4·2	3·5
Length of longest pinnules	52+	35	10
Number of segments in longest pinnules	50+	40	14

Only a short piece of the proximal part of the stalk remains attached to the calyx of the holotype. It emerges at a slight angle so that the two topmost columnals are incomplete on the posterior side. The sutures between the columnals are very irregular and undulating, often with isolated pockets in notches having some tendency to form vertical series and representing incipient intercalary segments. Just below the basal articulation is a ring of ten tubercles, which alternate with ten hollows in the basals. The very top of the stalk is slightly flared.

The basal ring is inverted conical, sloping fairly evenly anteriorly but slightly concave in posterior profile with a small bulge at the base. The three sutures lie approximately in radii B, C and E (see Fig. 1a), producing a small plate opposite interradius BC. The radial ring is much more asymmetrical, inclined posteriorly so that in side view it resembles the sloping headdress of the celebrated model of Queen Nefertiti, the posterior profile forming an almost straight line with the basal ring, whereas the anterior one makes an angle of about 140°. There is also some lateral compression so that the maximum diameter antero-posteriorly is distinctly greater than that at right angles to it. The radials curve inwards at the top all round so that the bases of the arms are vertical. There is a slight median convexity up each radial.

The individual arms are much narrower than the radials, being separated by more than their own width. The first brachial is partially occluded by the upper edge of the radial, so that it is shorter than the immediately following brachials, though these are short in comparison to the more wedge-shaped brachials that

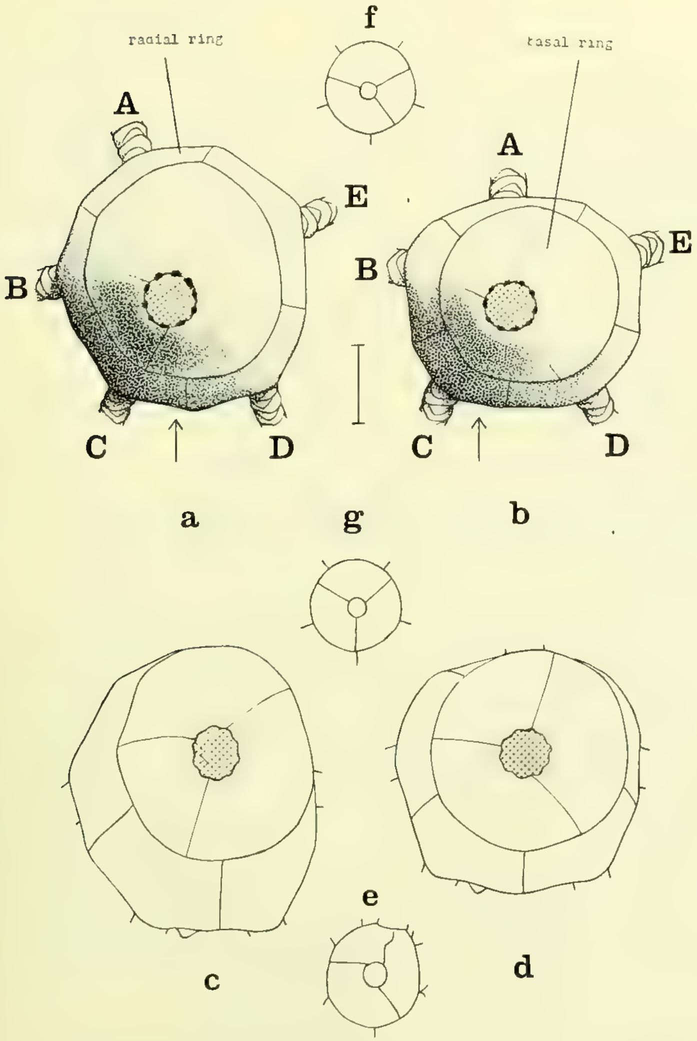

FIG. 1. a–e. *Anachalypsicrinus nefertiti* gen. & sp. nov. a and b. Holotype and large normal paratype viewed obliquely from below (the position of the stalk shown by cross-hatching) to show the sutures in the basal and radial rings [the scale equals 5 mm]. c and d. The same viewed vertically from below (parallel with the axis of the top of the stalk) showing the posterior offset of the radial ring. e. Basal ring of the abnormal paratype similarly. f and g. Diagrams of the basal rings from below of the holotypes of *Hyocrinus bethellianus* and *Thalassocrinus pontifer* drawn from descriptions.

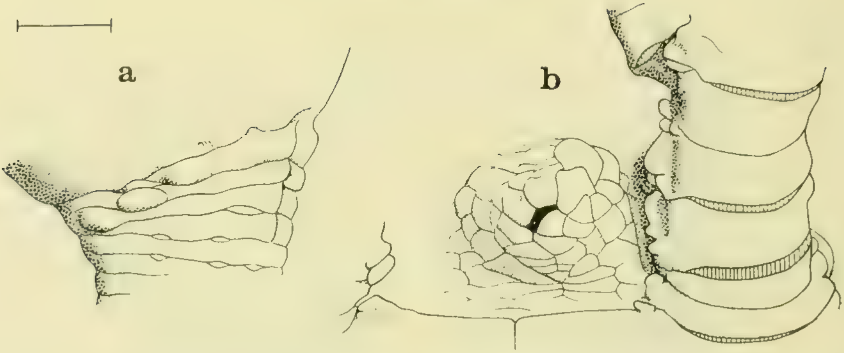

FIG. 2. *Anachalypsicrinus nefertiti.* Holotype. a. Junction of calyx and stalk from the side. b. Posterior edge of tegmen (interradius CD) showing anal cone and base of right posterior arm (C). [The scale equals 2 mm.]

follow. Br_3 is the only proximal brachial with a muscular articulation at each end, otherwise syzygies occur alternately, i.e. at 1 + 2, 4 + 5, 6 + 7, etc., though in the distal parts of the arms occasional instances occur of two consecutive muscular joints.

Although some of the arms are broken, there appears to be a size difference between the anterior and posterior ones, the latter being somewhat shorter and more slender. The breadth at brachials 4 + 5 is 3·2 mm on arm A but only 2·5 mm on arms C and D. [The paratype, specimen two, has a complete left anterior arm (E) 126 mm long, compared with *c.* 110 mm for one of its posterior arms.]

The first pinnule (which can be called P_2) is on the left side of Br_5 in each case. An intact one has 38 segments and measures 30 mm, though the immediately following pinnules are markedly longer. All the proximal pinnules have a smooth genital expansion from the third or fourth segment to the twelfth or thirteenth; this is enclosed partly by the pinnulars and partly by the series of rectangular side plates which stops abruptly at the end of the gonad. The ambulacra are supported by a series of smaller petal-like cover plates, three or four pairs of which correspond to each pinnular. The second to fourth pinnulars bear abruptly projecting lateral flanges. The joint between the first two pinnulars is capable of considerable vertical flexure, whereas those of the remaining segments are almost rigid. The genital area of each pinnule has a low rounded keel dorsally, lacking on the more distal segments.

The disc plating is most obvious on the anal cone (Fig. 2b) which is slightly offset in interradius CD towards the right posterior arm, C. The triangular interradial areas are sunken between the ambulacra and in each one there are up to 100 small, rounded papillae, projecting to various degrees, perforated individually by the water pores. In the concavity of the high, flange-like oral plate at the apex of each area there are one or two taller papillae and usually at least one capitate papilla or spinelet. Radially the disc ambulacra merge into the arms at about the sixth brachial.

There are a number of free-living myzostomes among the pinnules.

Paratypes. A large piece of stalk, broken at both ends, longer than those attached to the calyces, is included in the sample. It measures 155 mm in length, 3·75 mm in breadth and has 155 discoidal segments, the sutures between them rather irregular. At one end there is a fairly regular alternation of thick segments with intercalary thinner ones but the size evens up along the length of the piece. Very little flexure appears possible. The small specimen has the more distal (i.e. lowest) remaining columnals relatively long, 0·7 mm in height and 1·0 mm in diameter, but the upper segments are shorter, there being an abrupt change in length at about the fiftieth segment from the calyx. The upper extremity of the stalk is much less ornamented and fluted in the small specimen than in the larger ones.

The positions of the interbasal sutures (see Fig. 1a) agree in the small specimen with the holotype but the normal adult paratype (specimen two in Table 1) and the deformed specimen both have sutures in radii A and D instead of C and E, only the suture in radius B being common to all four specimens. Specimen two also differs from the holotype in the alignment of the maximum diameter of the radial ring. Although this in general slopes posteriorly, it is widest between radius E and interradius BC, almost at right angles to the antero-posterior plane. The small specimen (number three) does not show any distinct asymmetry.

As might be expected, the small specimen has the brachials relatively longer than in the others, the first three almost as long as broad (measuring median breadth rather than the expanded articular breadth) and the brachials after the sixth are longer than broad. It is preserved with its arms almost straight and vertical, only the very tips curling over. The total height of calyx and arms is 28 mm. It has six or seven pinnules on each side of each arm and the last three in each series are progressively shorter so that each ends about level with the arm tip. No gonads are evident.

The deformed specimen has the whole anterior half of the calyx bulging and covered with an irregular mosaic of plates. Only the two arms on the right side are normally developed; the two on the left are reduced and basally contiguous, one being twisted, while the anterior arm is completely absent.

A specimen of *Trichometra* was found attached by its cirri to the loose piece of stalk.

Affinities. *Anachalypsicrinus nefertiti* is clearly closely related to the four genera currently included in the subfamily Hyocrininae. In comparison with these it agrees only with *Thalassocrinus* in having a combination of: separate basals, the second syzygy situated at brachials 4 + 5 and the first pinnule on Br_5. The positions of the interbasal sutures may approximate in *Thalassocrinus pontifer* to those in the holotype of this new species (A. H. Clark's description is not very precise but there is evidently a suture approximating to radii B and E, though the third is said to be in the posterior *interradius*, matching with the interradial suture in CD). *Ptilocrinus* and *Gephyrocrinus* have fused basals, the second syzygy at 5 + 6 and the first pinnule on Br_4. *Hyocrinus* does agree in having distinct basals (though with sutures aligned like a mirror image of those of the holotype of *Anachalypsicrinus nefertiti*) but its second syzygy is at 3 + 4 and the first pinnule on Br_6; also the arms of *H. bethellianus* are much more slender relative to the width of the radials and the brachials are longer, even allowing for the smaller size of the described specimen – top stalk diameter 1·25 mm, while the anus is placed towards the left posterior arm, not the right. The holotype of *Thalassocrinus pontifer*, from the East Indies (Fig. 3) has the minimum stalk diameter just below the flared top 1·8 mm and the calyx *c.* 5·5 mm high, being considerably smaller than the two largest specimens of *Anachalypsicrinus*. This might account partially for the almost perfect radial symmetry of *Thalassocrinus* but the difference in this character coupled with the more laterally directed arms justifies a generic distinction in my opinion.

Geographically, the closest relative is *Gephyrocrinus grimaldii*, from the vicinity of the Canary Islands and Madeira, the holotype of which has the top stalk diameter only 1·0 mm, close to that of the smallest specimen of *A. nefertiti*. Unfortunately, Koehler's illustrations are poor but *G. grimaldii* evidently has the arms much less well marked off from the radials, while the ornamentation of the top of the stalk is considerably greater than in the small *A. nefertiti*, apart from the fused basals and different positions of the second syzygy and first pinnule.

Thalassocrinus pontifer A. H. Clark

(Fig. 3)

Thalassocrinus pontifer A. H. Clark, 1911 : 473–476 ; 1915, fig. 145.

The figure has been made from a rough sketch of the calyx of the holotype and only known specimen. It omits details of the tuberculation at the top of the stalk and on the tegminal plates. The interbasal sutures, described by A. H. Clark as ' almost obsolete ' are not shown. The narrow bands at the edges of the radials (shown stippled) are slightly darker than the rest in the preserved specimen and give the impression of being bevelled, though I did not think them depressed as A. H. Clark described. Possibly they indicate recent growth.

Family **PHRYNOCRINIDAE** A. H. Clark

Phrynocrinidae A. H. Clark, 1907 : 510 ; Gislén, 1925 (part) : 92.

The family was established by A. H. Clark, without diagnosis, to accommodate his new genus *Phrynocrinus*, type-species *P. nudus* from southern Japan. This was distinguished by having the stalk terminating below in a lobed attachment disc and above in only one or two discoidal columnals, all those in between being trapezoidal in shape (viewed from the side), broader than high, all joined by flexible synarthrial articulations of which the successive ones are flattened in alternate planes approximately at right angles so that they appear to be paired, the calyx

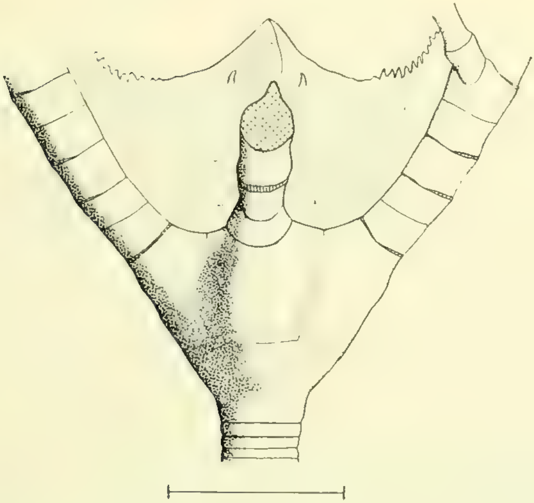

FIG. 3. *Thalassocrinus pontifer* A. H. Clark. Holotype. U.S. National Museum cat. no. 24783. Side view of calyx, adjacent ossicles and tegmen; the basal sutures not shown. The foremost arm is broken at Br_3. [The scale equals 5 mm.]

very squat and markedly flaring above, the arms diverging from the base leaving exposed extensive interradial areas of the tegmen or disc, relatively few syzygies present and no pinnules developed before the eighth or ninth post-radial ossicle, also branching occurs irregularly after the twelfth post-radial ossicle. The holotype of *P. nudus* is relatively large, the diameter of the topmost columnals 6 mm.

Two further genera, both monotypic, have since been referred to the family, namely *Naumachocrinus* A. H. Clark, 1912, type-species *N. hawaiiensis*, and *Porphyrocrinus* Gislén, 1925, type-species *P. verrucosus*, from the Kei Islands. Both of these genera have more or less numerous discoidal columnals proximally, the calyx elongated and approximately cylindrical, not appreciably wider than the top of the stalk, also the arm bases closely apposed laterally, continuing the vertical alignment of the radials. In fact, the general appearance is very like that of the Bathycrinidae, though some of the distal columnals with their compressed joints aligned in alternate planes are common also to *Phrynocrinus*. The arms of *Naumachocrinus hawaiiensis* are unknown beyond the first brachial and in *Porphyrocrinus verrucosus* the termination of the stalk is unknown. However, new material congeneric with *P. verrucosus* shows that the distal end of the stalk in this genus also terminates in a lobed disc. The bathycrinids are distinguished by the root-like ending of the stalk distally, with numerous irregular branching radicular ' cirri '. This precludes the inclusion of *Porphyrocrinus* and *Naumachocrinus* in the Bathycrinidae, if they are to be excluded from the Phrynocrinidae, which I am convinced must be done. It therefore becomes necessary to establish a new family to accommodate these two genera.

Since Gislén's diagnosis of the Phrynocrinidae allowed for the inclusion of *Porphyrocrinus*, a modified one follows.

Diagnosis. A family of Articulata with the stalk round or elliptical in cross section, without cirri, even the topmost columnals linked by flexible synarthrial joints and only the most proximal one or two sufficiently short in adults as to be termed discoidal (though in immature specimens the uppermost segments are relatively shorter and several may be discoidal), only one new columnal developed at a time immediately below the calyx, the remaining segments giving a moniliform appearance owing to the compressed elliptical joints alternating in alignment, attached to the substrate by an expanded terminal plate ; the calyx inverted conical in shape, relatively short and compact, the sutures between the five basals and five radial plates distinct, the two rings not widely dissimilar in height ; the division series following the radials similar in width basally to the radials but diverging abruptly, exposing the large tegmen (or disc) to view, ten arms (possibly more) in the two known genera, most syzygies separated by two or three muscular joints ; pinnules lacking basally from the first two or three possible positions on each side, the more proximal ones not markedly enlarged and with only small rods in the ambulacra, no conspicuous side or cover plates.

Phrynocrinus nudus A. H. Clark

(Fig. 4)

Phrynocrinus nudus A. H. Clark, 1907 : 507–510, fig. 1.
Phrynocrinus obtortus Matsumoto, 1913 : 221.

A sketch of the calyx of the holotype of *P. nudus* in the U.S. National Museum shows that in fact there are short vertical interbasal sutures and the individual basals are not really triangular as described by A. H. Clark, though he did note that the angles are blunted. The diameter of the top of the stalk is 6 mm, compared with 4 mm in the holotype of *P. obtortus* Matsumoto, also from southern Japan, and I think that this size difference is sufficient to account for the more obviously pentagonal shape of the basals in the latter. Judging from the material of a new member of the family described below, there may be some variation in the shapes of the columnals and the exact alignment of the successive stalk joints, which characters Matsumoto also used to try to distinguish his nominal species. Taking all this into account, including the geographical proximity of the type-localities, I consider that only a single species should be recognized and accordingly refer *P. obtortus* to the synonymy of *Phrynocrinus nudus*.

ZEUCTOCRINUS* gen. nov.

Diagnosis. A genus of Phrynocrinidae with only the more proximal columnals markedly trapezoidal in side view with compressed alternating joints, the more distal ones becoming cylindrical (the distal termination of the stalk unknown) ;

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* From Greek *zeuctos* - yoked or joined in pairs, referring to the appearance of the columnals.

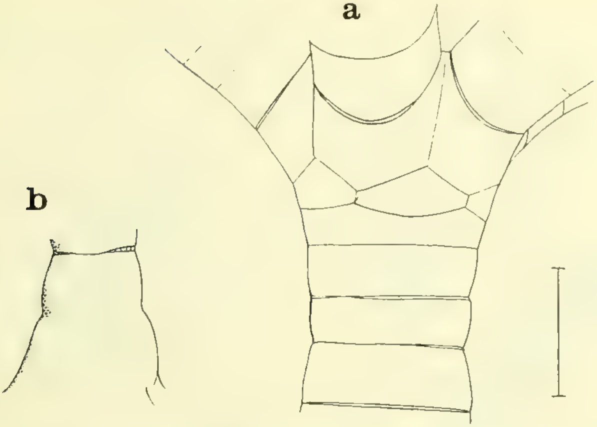

FIG. 4. *Phrynocrinus nudus* A. H. Clark. Holotype. U.S. National Museum cat. no. 22601. a. Side view of calyx and adjacent ossicles. b. Junction point of distalmost columnals and terminal stalk plate, showing the absence of a distinct suture at the last constriction, contrary to A. H. Clark's fig. 1D. [The scale equals 5 mm.]

the division series consisting normally of only two ossicles of which the IBr_1 in adults are proximally contiguous laterally but not in immature specimens, the two ossicles joined by syzygy; brachial syzygies normally at 1 + 2, 3 + 4, 7 + 8, 13 + 14 and then probably at intervals of three or four muscular joints; pinnules not developed in the first three possible positions, the first one being P_4 on Br_{10} or thereabouts.

TYPE-SPECIES. *Zeuctocrinus gisleni* sp. nov.

Zeuctocrinus gisleni sp. nov.

(Fig. 5. Pl. 2)

MATERIAL. 'Discovery' Investigations st. 7711/66; 53°11·2′ N : 20°5·1′ W–53°11·6′ N : 20°3·9′ W (North Atlantic, *c.* 400 nautical miles west from Northern Ireland), 2432–2380 metres. Holotype [B.M. reg. no. 1972.12.5.4] and four paratypes.

DIAGNOSIS. As for the genus.

DESCRIPTION. All the specimens have the stalk broken, so that their distal ends and attachments are unknown.

The holotype (Fig. 5a, b, Pl. 2 figs. a, b) is the largest specimen, number 1 in Table 2. It has the topmost columnal only partially developed and almost discoidal but the second one is already more than half as high as its minimum diameter. Together they form a prominent synarthrial tubercle on one side, though the

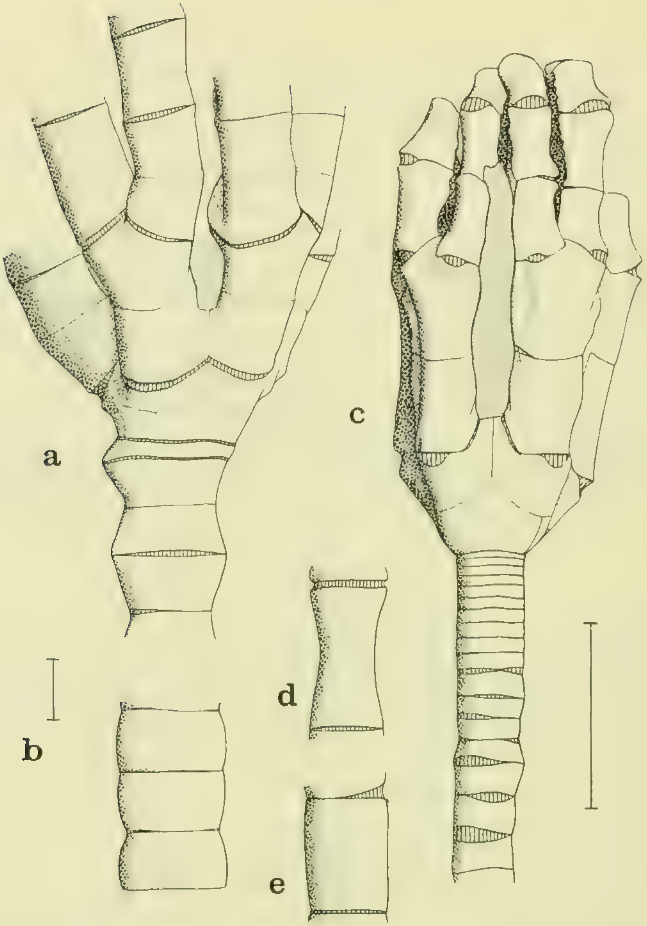

FIG. 5. *Zeuctocrinus gisleni* gen. & sp. nov. a and b. Holotype. a. Calyx and adjacent ossicles. b. Distal most remaining three columnals (numbers 31–34 from top) c–e. Smallest paratype. c. Crown and proximal part of stalk. d. Columnal 52. e. Columnal 59. [Both scales equal 2 mm ; that on the right applies to c–e.]

opposite side is still flat. The next 25 or so segments have their joints symmetrically elongated in alternate planes almost at right angles (in fact the plane of elongation spirals through 90° during about six pairs of articulations). This produces a moniliform appearance to the stalk in side view, with the segments forming pairs. The modification in shape gradually lessens distally so that the last few columnals are almost cylindrical.

TABLE 2

Numerical data from the holotype (1) and four paratypes of *Zeuctocrinus gisleni* sp. nov. Measurements are in millimetres.

	1	2	3	4	5
Stalk:					
Length remaining	61	50	50	57	58
Number of segments remaining	34	26	40	50	62
Number of segments in top 10 mm	7	8	10·5	18	27
Length of top 10 segments	16	14	9	4	1·7
Length of lowest remaining segment	2·0	2·3	1·3	1·7	1·2
Maximum diameter at lower end	3·6	2·5	2·2	1·3	0·8
Minimum diameter near top	2·8	2·0	2·0	1·2	0·7
Calyx:					
Diameter of lower end of basals	3·6	2·6	2·4	1·2	0·7
Diameter of top of radials	5·2	4·2	3·7	2·4	1·8
Maximum height radially	1·9	1·7	1·7	1·1	0·6
Post-radial series:					
Length IBr$_1$	2·2	1·8	1·5	1·2	0·8
Length IBr$_2$	2·8	2·4	2·3	1·5	1·3
Median breadth IBr series	2·6	1·7	1·7	1·0	0·7
Breadth at 3 + 4	2·2	1·5	1·7	0·8	0·4
Length IBr$_1$ to 3 + 4	9·4	7·9	7·0	5·0	3·9

The calyx is distinctly asymmetrical (Fig. 5a), lowest in radius E (the left anterior one viewing orally). The general skin-covering seems particularly opaque in this area and the sutures can only be seen by dissolving it in bleach – and then only very indistinctly. The suture between the basal and radial rings forms a zig-zag line. The interbasal and interradial sutures are approximately equal in height since the latter are cut short by the meeting of the adjacent IBr$_1$ interradially; the interradial calyx height is *c.* 2·7 mm. The division series and arms are almost cylindrical in cross section. The two ossicles of the division series (in one case four) are joined by syzygy.

All the arms are broken by or at the fourth syzygy, which is usually at 13 + 14 but in one case each at 12 + 13 and 14 + 15. The previous syzygies are at 1 + 2, 3 + 4 and 7 + 8 except on the pair of arms based on the IIBr series of four ossicles, which have syzygies at 2 + 3, 4 + 5 and 8 + with a pinnule on the *inside* of Br$_6$. All the other arms remaining beyond Br$_8$ have the first pinnule (P$_4$) on the outside of Br$_{10}$. It has 9 + (? *c.* 3) evenly tapering segments and measures 5·9 + mm in length (probably + *c.* 2·0 mm).

The tegmen (disc) is joined to the arms to about Br$_7$ while the prominent anal cone reaches level with Br$_{12}$.

PARATYPES. Specimen 2 has the top columnal fully developed, forming a perfect inverted pair to the second one. The successive joints are again aligned at not quite 90° so that there is a slight spiralling effect of the joint faces. The calyx again is somewhat asymmetrical but in this case the anterior radius, A, is the lowest. The IBr series are not quite in contact laterally, allowing the radials to be seen interradially to a height of 3·3 mm. There are slight lateral flanges on the proximal brachials. The longest remaining arm has 21 segments left, measuring 21 mm in length; when intact it was probably about as long again. The breadth at the distal end is 1·2 mm as opposed to 1·5 mm at 3 + 4. The positions of the syzygies are very irregular and in only one or two cases does the joint between brachials 1 and 2 appear to be a proper syzygy, though 3 + 4 is developed on each arm. In one case the next syzygy is not until 13 + 14, followed by 17 +, while another has 1 + 2, 3 + 4, 6 + 7, 9 +. One arm even has two successive syzygies, 3 + 4 + 5 (as described by A. H. Clark in the holotype of *Phrynocrinus nudus*), followed by 8 + 9 and 12 +. P_4 on Br_{10} is normally the first pinnule again, though there is a pinnule on Br_7 in one case and on Br_9 or Br_{11} in two others. P_4 has 14-18 segments, the basal ones stout, though longer than broad and flared at the joints, while the distal segments are attenuated. The length is 6·5 8 mm. P_5 may bear a small gonad near its base. There are some very slender and often branching rods in the ambulacra. One pinnule is bifurcated near its base.

Specimen 3 has several of the topmost columnals relatively short. The calyx is not appreciably asymmetrical. The sutures between basals and radials are distinct, even when wet, owing to a slight bevelling of the edges. The division series are again slightly spaced laterally. All the arms are broken by or at the fourth syzygy; the syzygies remaining are at 1 + 2, 3 + 4, 7 + 8 and 12 or 13 +, with the first pinnule on the outside of Br_{10}.

Specimen 4 has the four topmost columnals discoidal, while the lower ones conversely are much longer relatively than in the larger specimens and are medially constricted with length : median breadth 1·6 : 1. It too has the sutures in the calyx distinct by virtue of being bevelled at the edges. The maximum height of the basals is *c.* 0·8 mm. No appreciable asymmetry is present. The division series are separate laterally and have slight lateral flanges, continued on to the arm bases.

The smallest specimen (Fig. 5c–e) shows these same tendencies even better developed. Up to 11 of the uppermost columnals are discoidal and the distalmost are only just cylindrical, not stouter medially, while the longest segments have length : median breadth as much as 2·5 : 1. The upper segments are so short that the usual moniliform appearance is not obvious. The division series are widely spaced laterally and there are very marked lateral flanges on them and on the first few brachials.

The main ontogenetic changes can be outlined as follows: The younger specimens have a great disparity in the relative length of the upper (short) and lower (long) columnals. The basals and radials become relatively broader in larger specimens and the calyx takes on some degree of asymmetry, though it remains to be seen if this has an antero-posterior correlation. The division series are at first widely separated laterally at their bases but gradually approximate, to become contiguous when the basal diameter of the calyx exceeds about 3 mm; they have prominent lateral flanges, continued on to the arm bases, but these gradually become obsolete and the ossicles more nearly cylindrical.

Affinities. In comparison with *Phrynocrinus*, the only other genus included in the family as here restricted, *Zeuctocrinus* differs in having the more distal columnals much less moniliform and the division series limited, normally to only two ossicles.

Family **PORPHYROCRINIDAE** nov.

The justification for establishing this new family is given in the discussion of the Phrynocrinidae above.

Diagnosis. A family of Articulata with a rounded stalk, without cirri, with several of the proximal columnals discoidal and inflexibly jointed by synostosis but with new segments formed only between the topmost one and the calyx, the middle columnals elongated and more or less cylindrical (sometimes barrel-shaped or else waisted), with synarthrial joints which distally become elliptical, alternating in alignment, giving a moniliform appearance, attached to the substrate by an expanded terminal plate ; the calyx probably thick-walled, relatively small and more or less cylindrical, not markedly flared at the top, the basals slightly or very much shorter than the radials ; the arms continuing the alignment and width of the radials, closely approximating laterally and obscuring the tegmen (or disc) from lateral view, syzygies alternating usually with muscular joints and pinnules lacking basally from the first two or three possible positions on each side of the undivided arms, none markedly enlarged and all lacking conspicuous side or cover plates. [The syzygies and pinnules unknown in *Naumachocrinus*, the arms of the only known specimen being broken after the first brachial.]

Included genera. *Porphyrocrinus* Gislén, 1925, type-species *P. verrucosus* Gislén, 1925 ; hitherto monotypic.

Naumachocrinus A. H. Clark, 1912a, type-species *N. hawaiiensis* A. H. Clark, 1912a ; monotypic.

PORPHYROCRINUS Gislén

Porphyrocrinus Gislén, 1925 : 91–92.
? *Monachocrinus* (part ; *M. incrassatus*) Gislén, 1933 : 483–485.

The type-species, *Porphyrocrinus verrucosus* Gislén is only known from a single specimen taken near the Kei Islands (*c.* 5·5° S : 133° E) in 345 metres (a relatively small depth for a stalked crinoid). It lacks the distal end of the stalk so the form of attachment is unknown. As discussed under the heading of the Phrynocrinidae, I consider that Gislén was mistaken in referring it to that family. The general facies with closely apposed arms arising from the nearly cylindrical calyx without abrupt distinction and the discoidal, rigidly articulated, proximal columnals giving way distally to more or less cylindrical segments (though these are somewhat compressed at the joints in alternating planes), is far more like that of the Bathycrinidae than of the Phrynocrinidae.

Another specimen which I think will prove to be referable to *Porphyrocrinus* is the holotype (and only known specimen) of the supposed bathycrinid *Monachocrinus incrassatus* Gislén, 1933, from St Helena, in which only one ossicle remains above each radial. Gislén discarded the idea of its affinity with *Porphyrocrinus* because in that genus ' the upper part of the stem is not thickened and the distal stem-joints only very gradually reach the type of long slender knobby stem-joints which is so well developed in most Bathycrinidae and all Monachocrini. Besides this, all the Phrynocrinidae [with which he allied *Porphyrocrinus*] are large and stout forms, while the new species just as the Bathycrinidae is a small and slender form.' Although the holotype of *Phrynocrinus nudus* was certainly much larger, the diameter at the very top of the stalk 6 mm, the same measurement in the holotype of *Porphyrocrinus verrucosus* is only 1·5 mm, compared with 0·8 mm in the holotype of *Monachocrinus incrassatus*. It seems to me premature to assume that the last nominal species is a small one on the basis of a single specimen and I believe that the differences in the stalk could well be correlated with the smaller size. Since the species of *Monachocrinus* are characterized by having division series and ten arms, it remains for more nearly complete specimens to be collected in the vicinity of St Helena with either arms or division series present beyond the first post-radial ossicle and preferably also the entire stalk to show where its true affinity lies. The possibility that *M. incrassatus* can be referred to *Porphyrocrinus* is enhanced by two stalked crinoids collected in the southern Indian Ocean, about mid-way between South Africa and Amsterdam Island, in 400 metres. These have the diameter at the top of the stalk 1·2 and 1·3 mm. Although both have the post-radial series broken after the first ossicle, fortunately two loose arms are present with them, indicating that the first ossicle is Br_1 not IBr_1, though it is just possible that an intervening axillary and first brachial have been lost. These two specimens resemble *P. verrucosus* except that they have more numerous discoidal proximal columnals, the radials are relatively longer, though possibly within the range of specific variation, the first pinnule is on Br_{10} on both the loose arms, as in only one out of five arms of Gislén's specimens – the other four having a pinnule on Br_8, and the texture of the stalk is smooth throughout, though the verrucose distal part of the stalk of the Kei Islands species may be unnatural. The likelihood of these two specimens being conspecific with the holotype of *Monachocrinus incrassatus* is discouraged by the occurrence in the same haul of the bathycrinid *Democrinus chuni* – well known from South Africa, which is half-way to St Helena but where *Porphyrocrinus* has not been taken. It seems necessary therefore to distinguish a new species.

Porphyrocrinus polyarthra * sp. nov.

(Fig. 6a–g)

MATERIAL. Cape Town University no. AFR.A 1248I, 36°48′ S : 52°08′ E (southern Indian Ocean, about half-way between South Africa and Amsterdam

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* Many-joints, referring to the multiple consecutive rigid joints in the distal part of the stalk.

Island to the east), 400 metres.† Holotype with a complete stalk [to be deposited in the South African Museum], paratype [B.M.reg. no. 1972.12.5.7] incomplete distally, both lacking the arms after the first post-radial ossicle ; also present several detached pieces of stalk and two arms.

DIAGNOSIS. A species of *Porphyrocrinus* with the columnals smooth throughout, up to seven consecutive distal ones rigidly jointed by synostosis, usually immediately above the multilobate terminal plate ; numerous proximal columnals discoidal (*c.*17 when the topmost stalk diameter is 1·3 mm) ; calyx approximately cylindrical, but slightly constricted medially, flaring gently above and below (at least in the holotype and paratype but this may be subject to variation), the interbasal and interradial sutures distinct, the radials appreciably longer than the basals ; the first pinnule probably P_3 on Br_{10}.

DESCRIPTION. The holotype is the first specimen in Table 3. The distal end of its stalk terminates in a much expanded plate with finger-like lobes closely applied around a piece of scleractinian coral. The six distalmost columnals are rigidly united by successive synostoses, superficially appearing as an interrupted line like a syzygy. The disarticulated joint faces (Fig. 6g) show about 15 radiating shallow grooves around a large figure-of-eight-shaped concavity. The alignment of the stalk bends round through about 90° just above the terminal plate. Two segments with flattened, alternating, flexible synarthrial joints follow, their maximum breadth 2·1 mm. Then come five more consecutive synostosial joints succeeded by bollard-shaped segments about twice as long as their maximum (articular) breadths, the joints slightly elliptical in alternating planes, making up most of the length of the stalk. Towards the top (proximally) the columnals shorten so that the twenty-fifth one from the calyx is about as high as broad and the seventeenth and those above it can be called discoidal. At the very top the stalk broadens again after narrowing. There are about 90 columnals altogether and the length is *c.* 150 mm.

TABLE 3

Numerical data from the holotype (1) and paratype of *Porphyrocrinus polyarthra* sp. nov.

	1	2
Stalk :		
Number of discoidal proximal segments	17	11
Number of segments in top 5 mm	22	18
Diameter at extreme top (= bottom diameter of basals)	1·3	1·2
Minimum diameter just below top	0·9	0·9
Calyx :		
Diameter at top of basals	1·1	1·1
Diameter at top of radials	1·4	1·4
Height of basals (maximum)	0·8	0·6
Height of radials (maximum)	1·1	1·1

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† This locality is the highest point yet known on the South-west Indian Ocean submarine ridge.

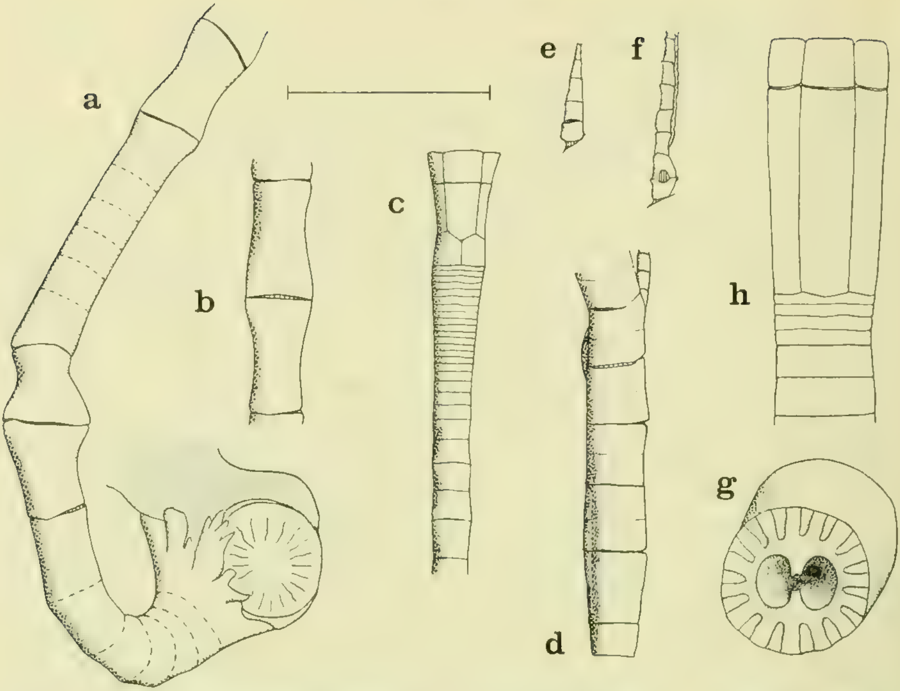

FIG. 6. a–g. *Porphyrocrinus polyarthra* sp. nov. a–c. Holotype. a. Distalmost part of the stalk attached to coral (stippled). b. Columnals 59 and 60 from top. c. Calyx with adjacent ossicles. d. Proximal part of loose arm from Br$_2$, showing bases of P$_3$ and P$_c$. e. P$_3$ (tip missing). f. P$_9$ (tip missing). g. Face of distal synostosial joint from large broken stalk fragment. h. *Naumachocrinus hawaiiensis* A. H. Clark. Holotype. U.S. National Museum cat. no. 29573. Outline of calyx with adjacent ossicles. [The scale equals 5 mm for a–f and h and 2 mm for g.]

The calyx is very slender and slightly constricted at the upper end of the basals, though the radials flare out at the top, this even flaring being continued by the first brachials, which are broader than long. The sutures in the calyx are distinct, those between the basal and radial rings making a zig-zag line.

Two detached arms were found in the crinoid debris taken at this station which are very likely to have come from this specimen or the paratype. [Although *Democrinus chuni* was also collected, its arms differ in tapering from Br$_3$ and have the first pinnule on Br$_6$.] The first ossicles on both these two arms have a syzygy on the proximal face and their breadth corresponds with that of the distal end of the first post-radial ossicle still attached to the calyx, so I am fairly confident that they can be regarded as Br$_2$s. They expand to a maximum breadth of 1·5 mm at Br$_5$, having well-marked lateral flanges, and only very slowly taper distally. Both measure *c.* 40 mm in length. Syzygies and muscular joints normally alternate from 1 + 2, 3 + 4 onwards but one of the two arms has extra muscular joints at 13 – 14, 46 – 47, 53 – 54 and 58 – 59, though the other only has one such joint at 59 – 60. The last brachial remaining in both is Br_{66}, ending in a syzygy and showing no terminal modifications. The first pinnule is on the left side of Br_{10} and can be regarded as P_3. It probably had six or seven segments and a fairly attenuated tip tapering from a stout base; the joint between the first two segments is particularly flexible and this is even more true on the subsequent pinnules (see Fig. 6e and f).

PARATYPES. The distal ends of two other stalks are present. One has the lobes of the terminal plate almost meeting around a cylindrical piece of coral and only two of the consecutive distalmost segments jointed by synostosis, though three further ones are similarly jointed after an interval of several synarthrial joints. The other is stouter and has the six distalmost joints rigid, curving through 90° as in the holotype. The surface of all these pieces of stalk is quite smooth. The calyx with incomplete stalk is very similar to that of the holotype except for having fewer discoidal proximal columnals.

AFFINITIES. The affinities of these specimens and justification for describing them as a new nominal species are recounted in the discussion of the genus *Porphyrocrinus*. However, the use of the number of discoidal proximal columnals as a character of specific weight needs some qualification. Gislén (1925) counted nine of the topmost columnals of the holotype of *Porphyrocrinus verrucosus* as discoidal but I would say that the ninth one was already too thick to be so described, at least judging from his figure 2, leaving only 8 compared with 11 and 17 in the two slightly smaller specimens of *P. polyarthra*. Even so, the wide variation in these two and the likelihood that the number of discoidal proximal segments decreases with growth (as it does in bathycrinids and phrynocrinids) combine to suggest that this difference may not be significant. The holotype of *P. verrucosus* lacked the distal extremity of the stalk beyond the eighty-sixth columnal and Gislén only observed one distal synostosis, between segments 33 and 34. However, it is just possible that more distal ones were overlooked since the last 30 segments had their articulations obscured by the 'verrucose' surface texture (though the shape should have indicated any absence from the usual alternating synarthrial jointing). If more nearly complete specimens from the vicinity of the Kei Islands also prove to show multiple distal synostoses and if the peculiar texture of the distal part of the stalk of the holotype of *P. verrucosus* turns out to be abnormal, then the distinction of two species will be difficult.

Naumachocrinus hawaiiensis A. H. Clark

(Fig. 6h)

Naumachocrinus hawaiiensis A. H. Clark, 1912a: 195–197; 1915, fig. 129.

A figure of the calyx of the holotype in the U.S. National Museum is given here, since it is very small in Austin Clark's figure. I could not detect the very short interbasal sutures. The basal ring is 0·3–0·4 mm high; the decimal point was omitted in A. H. Clark's description.

Family **BATHYCRINIDAE** Bather

Bathycrinidae Bather, 1899 : 922 ; Gislén, 1924 : 206–212 ; 1927 : 53–54 ; 1938 : 3–14 ; A. M. Clark, 1970 : 13.

Although a number of diagnoses for this family have already been given (including one of my own which was largely comparative with the fossil Bourgueticrinidae), a modified version for comparison with those for the three preceding families may be useful.

Diagnosis. A family of Articulata with a rounded stalk, without true cirri, with some of the proximal columnals discoidal and inflexibly jointed by synostosis but with new segments formed only between the topmost one and the calyx, the middle columnals elongated and more or less cylindrical (sometimes barrel-shaped or else waisted), with synarthrial joints which distally become elliptical, alternating in alignment, giving a moniliform appearance, attached to the substrate by irregular, branching, jointed, radicular ' cirri ' arising from several of the distalmost columnals ; the calyx thick-walled, relatively small and rather variable, ranging from almost cylindrical to inverted conical, the basals either separate or fused together, longer or shorter than the radials, which may also be distinct or occasionally fused with the basals ; the division series or arms following the radials continuing the same alignment, closely approximating laterally and obscuring the tegmen (or disc) from lateral view, syzygies numerous, mostly alternating with muscular joints though proximally there may be several pairs of successive muscular joints, pinnules lacking basally from the first two or three possible positions on each side of the arms, none markedly enlarged and all lacking conspicuous side or cover plates.

Remarks. This family is normally linked with the fossil Bourgueticrinidae in the suborder Bourgueticrinina on account of the root-like stalk attachment common to both (where known). However, the diagnosis just given is remarkably similar to that provided for the new family Porphyrocrinidae, except for the lobed attachment plate terminating the stalk in the latter (besides minor differences in the calyx). A thorough review of the relationships between the recent and fossil stalked Articulata is needed. Several of the families known only from recent material were omitted from the classification given by Ubaghs (1953). It is to be hoped that their affinities will be resolved by the long-awaited crinoid part of the *Treatise on Invertebrate Paleontology*.

Democrinus chuni (Döderlein)

Rhizocrinus chuni Döderlein, 1907 : 14–15, pl. 1 fig. 5, pl. 6 fig. 6.
Democrinus chuni : Gislén, 1938 : 26–27 ; A. M. Clark, 1972 : 146–150, fig. 17.

Material. Cape Town University no. AFR.A 1248I, 36°48′ S : 52°08′ E (southern Indian Ocean, about half-way between South Africa and Amsterdam Island to the east), 400 metres. One specimen.

Cape Town University no. ABD 11F ['Anton Bruun' cruise 7, st. 389C], 30°12′ S : 32°01′ E (off Durban), 1360 metres. One small specimen.

The specimen from the southern Indian Ocean has about 100 mm length of stalk still attached to the calyx; probably this represents only about half the total length. The calyx has an extra transverse suture across the basal ring at about three-quarters of its height.

The small specimen shows the usual immature inverted conical shape of the calyx. The stalk trifurcates at the twenty-fifth segment, about 10 mm below the calyx.

RANGE. The first record provides an extension of range for this species, otherwise known from east and south Africa.

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PLATE 1

Anachalypsicrinus nefertiti gen. & sp. nov.
- a. Holotype.
- b. Large normal paratype.
- c. Abnormal paratype.
- d. Small paratype. (All × 1.)

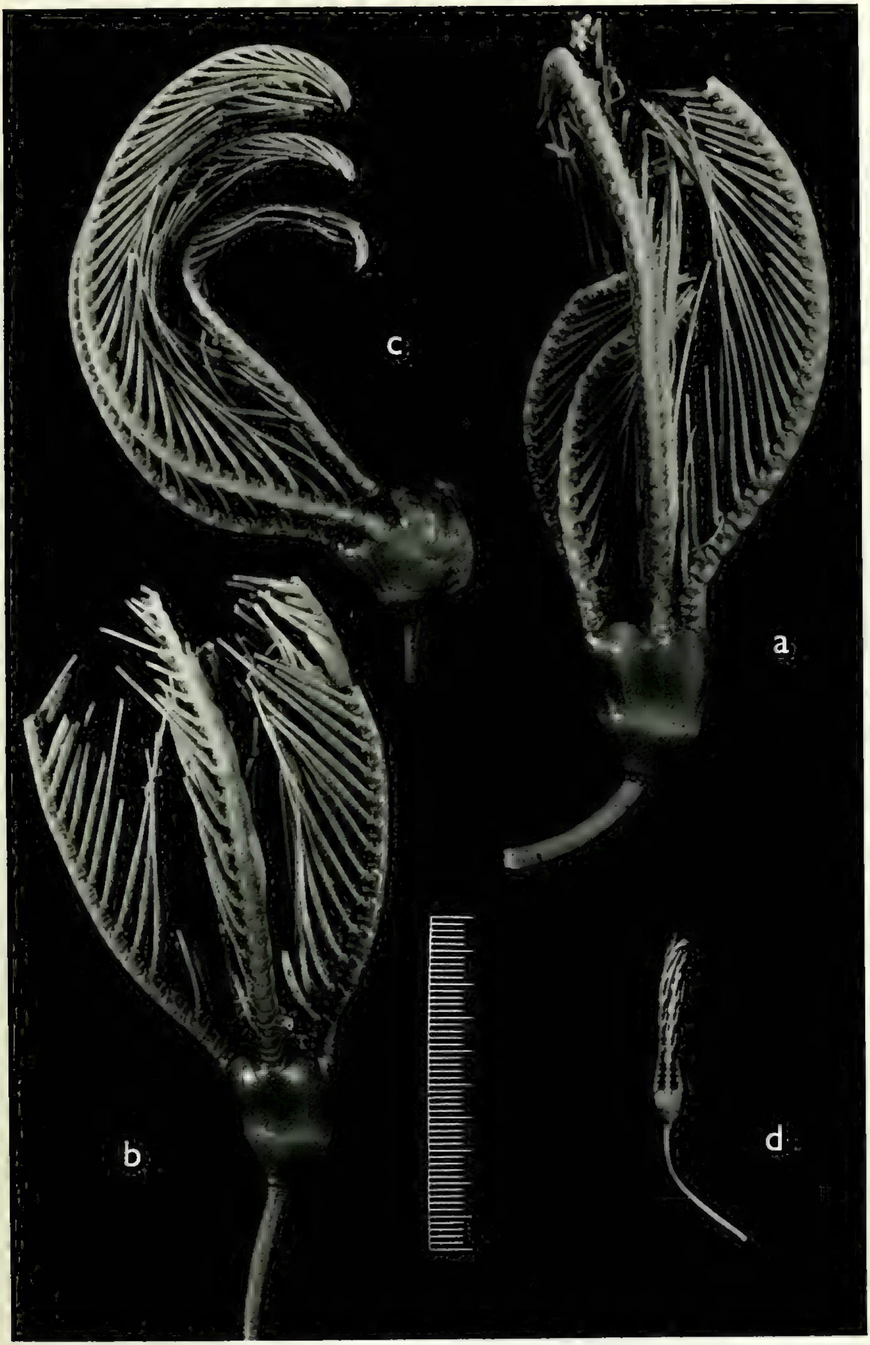
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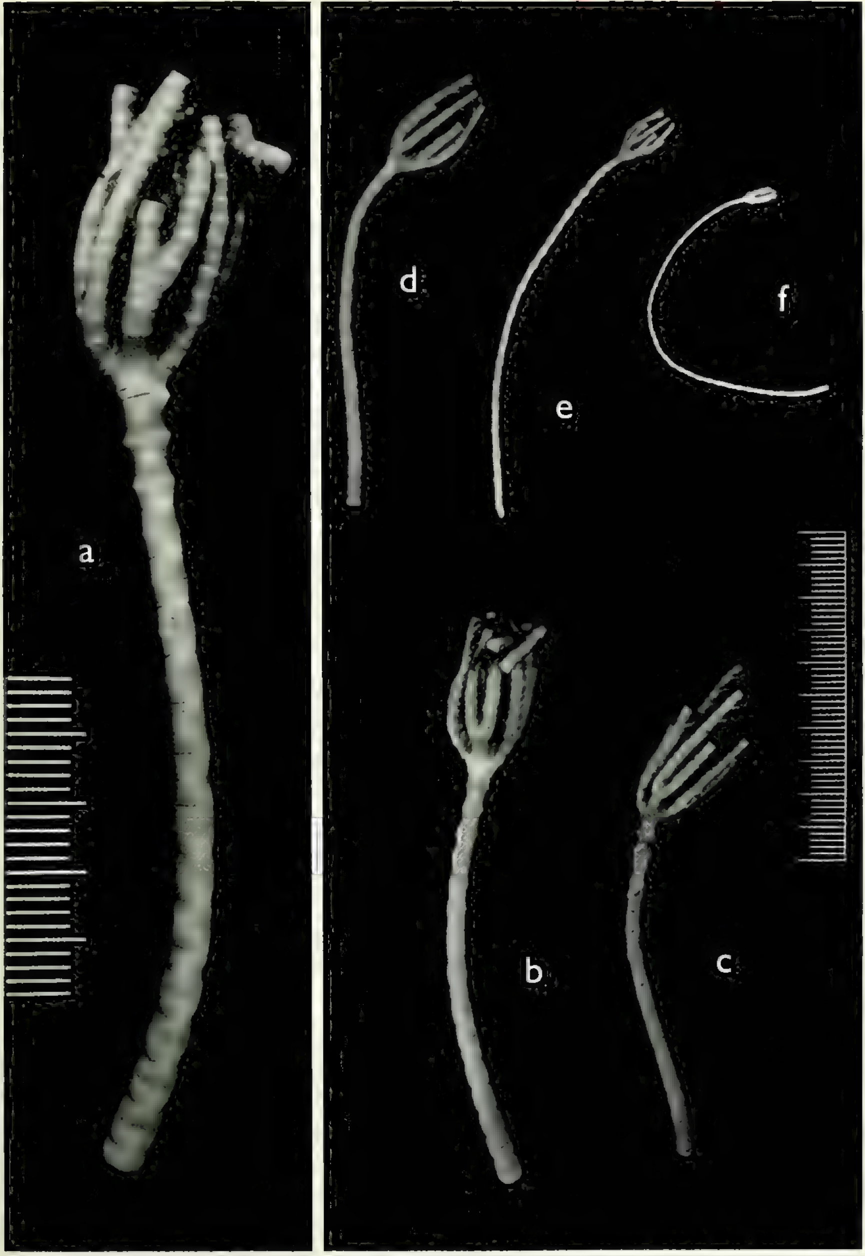
PLATE 2

Zeuctocrinus gisleni gen. & sp. nov.

a. Holotype, showing radius with division series of four ossicles (× 2).

b–f. Holotype viewed from opposite side and four paratypes (specimens 1–5 in Table 2) (× 1).


a
d
e
f
b
c

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Pp. 289–366 ; 15 *Text-figures*, 4 *Tables*

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By EDWIN NICHOLAS ARNOLD

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SYNOPSIS

It is pointed out that the equatorial and southern African species of *Lacerta* Linnaeus 1758 and *Algyroides* Bibron & Bory 1833 are not at all closely related to the palaearctic members of these genera. The present classification of the palaearctic species of *Lacerta, Algyroides* and

Psammodromus Fitzinger 1826 is discussed and found to be unsatisfactory in several respects. Characters available for grouping species are described, including a number of features (mainly skeletal and hemipenial) not employed before. Using ecological and functional data, an attempt is made to assess the lability of available characters : many of the external and cranial features used in ' classical ' lacertid systematics appear to be potentially labile and therefore must be given low comparative weight in judging relationships. Using this comparative weighting, it appears that *Algyroides* and *Psammodromus* are natural groups and that *Lacerta* is divisible into four main sections. Two of these will be retained in *Lacerta* (as *Lacerta* parts I and II) but the others are raised to the status of separate genera : *Gallotia* Boulenger 1916 and *Podarcis* Wagler 1830. Proposed systematic changes are listed in full on p. 357.

INTRODUCTION

At least fifty-five species are currently assigned to the genus *Lacerta*.* Of these, forty-nine are limited to a relatively small part of the southwestern Palaearctic region while two others, *L. vivipara* Jaquin and *L. agilis* Linnaeus, occur not only in this area but also range more widely in Eurasia (see Fig. 1). The remaining four members of the genus are found in Africa south of the Sahara desert. These are : *L. echinata* Cope (tropical forests of West Africa from Liberia to the eastern Congo Republic), *L. jacksoni* Boulenger (eastern Congo Republic, Uganda, Kenya and Tanganyika), *L. rupicola* Fitzsimons (Zoutpansberg, Transvaal, Republic of South Africa), and *L. australis* Hewitt (near Ceres in Cape Province, Republic of South Africa). *L. echinata* and *L. jacksoni* have strong affinities with their Central African neighbours in the genera *Algyroides*, *Bedriagaia* and *Gastropholis*, and *L. rupicola* seems to be most nearly related to *Tropidosaura*. It does not seem possible to retain these species in *Lacerta* and their precise relationships will be discussed elsewhere. *L. australis* is apparently known only from the single type specimen (which is not available to me) and is not well enough studied for its real affinities to be clear. But, on geographical grounds, it is not likely that *L. australis* is closely related to the Palaearctic species of *Lacerta* for the type locality is separated from the range of this assemblage by a hiatus of over 7000 km. In the rest of this paper, *Lacerta* will be used to refer only to the fifty-one Palaearctic species.

The classification of Palaearctic *Lacerta* has presented a number of difficulties. Many characters used in their systematics exhibit great intraspecific variation making the delimitation of species-boundaries difficult. Some of this extensive variation is geographic ; for instance, Mertens & Wermuth (1960) list no fewer than 31 subspecies of *L. erhardii*, 32 of *L. pityusensis* and 39 of *L. sicula* and many subspecies of the last have been recognized since (Brelih 1961, 1963, Lanza 1966, Lanza & Borri 1969, Mertens 1966). Many forms also show considerable intrapopulational variability especially in colour and pattern. Notwithstanding this, classification at the species level is now fairly stable thanks to the investigations of a long series of workers including Eimer (1881), Bedriaga (1886), Werner (1904),

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* This figure includes *Lacerta cappadocica* Werner which has sometimes been placed in a separate genus, *Apathya* Méhely, and four parthenogenetic forms allied to *L. saxicola* Eversmann, viz. *L. armeniaca* Méhely, *L. dahli* Darevsky, *L. rostombekovi* Darevsky and *L. unisexualis* Darevsky. It is very probable that several other species will eventually be recognized.

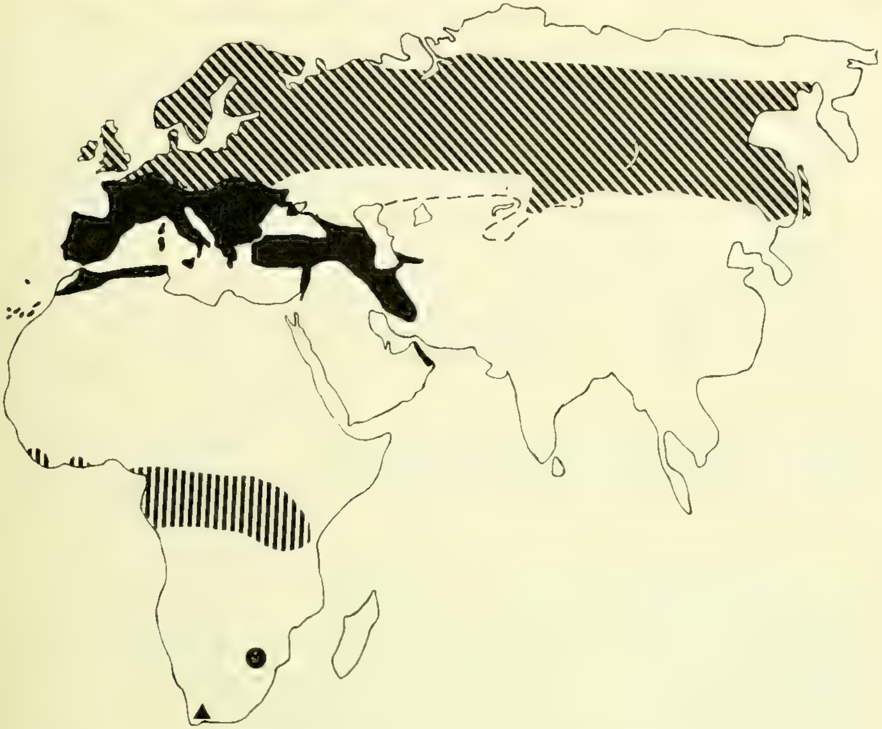

FIG. 1. Distribution of lizards usually assigned to *Lacerta*, *Algyroides* and *Psammodromus*. Black : area containing *Psammodromus*, European *Algyroides* and 51 species of *Lacerta* (49 of which are confined to the region marked). Diagonal hatching : distribution of *Lacerta vivipara* outside the main range of Palaearctic *Lacerta*. Broken line : distribution of *Lacerta agilis* beyond main range of Palaearctic *Lacerta* and of *L. vivipara*. Vertical hatching : combined distribution of '*Lacerta*' *echinata*, '*Lacerta*' *jacksoni* and the African species customarily assigned to *Algyroides*. Solid black circle : only known locality of '*Lacerta*' *rupicola*. Black triangle : only known locality of '*Lacerta*' *australis*.

Boulenger (1905, 1913, 1916, 1920), Méhely (1907, 1909, 1910), Schreiber (1912) and more recently Mertens (numerous publications mainly in *Senckenbergiana Biologica*), Klemmer (1957), Peters (1962a, b) and Darevsky (1957, 1966, 1967).

Problems still remain in defining acceptable species-groups within the genus, despite several attempts having already been made to divide *Lacerta* into subunits, and comprehensive schemes of classification having been put forward by Bedriaga (1886), Werner (1904) and Boulenger (1916). The last author divided the Palaearctic forms of *Lacerta* into five sections or subgenera : I – *Lacerta* s. str., II – *Gallotia* Boulenger, III – *Zootoca* Wagler, IV – *Podarcis* Wagler and V – *Thetia* Gray which is, in fact, a junior synonym of *Scelarcis* Fitzinger. Méhely (1907, 1909, 1910), who dealt only with the small, mainly climbing forms commonly known as Wall Lizards separated these into two groups, 'Archaeolacertae' and 'Neolacertae'. But Boulenger (1907, 1910) was very critical of Méhely's division and did not recognize it in his own classification when he placed all Wall Lizards in Section IV (subgenus *Podarcis*). Subsequent investigations, however, have supported Méhely's division and *Podarcis* of Boulenger is now divided into the subgenera *Podarcis* s. str. and *Archaeolacerta* Mertens, which are respectively more or less equivalent to Méhely's Neo- and Archaeolacertae. A seventh subgenus, *Apathya* Méhely, is sometimes recognized for *L. cappadocica* (e.g. by Mertens 1952).

This classification is not entirely satisfactory for the borders of some subgenera are not well defined and a number of species have either never been properly assigned to a particular subgenus or their position has been recently questioned. Furthermore, many of the characters by which the subgenera are distinguished are probably quite labile and on their own do not provide an adequate basis for arranging species into natural assemblages (see pp. 315). Such characters may turn out to delimit natural groups but confirmation from other features is necessary. At present, subgeneric classification is mainly based on external features plus a few variations in skull structure. It seems essential to re-assess these characters and, more important, to increase the range of variables available for classifying *Lacerta* and its allies. This increase should involve not only the absolute number of characters used but also the number of sources from which they come. For this reason, I have investigated the skeletal and hemipenial morphology of these lizards.

It seems convenient to discuss the relationships of two other genera in conjunction with *Lacerta*, namely *Algyroides* Bibron & Bory and *Psammodromus* Fitzinger. *Algyroides*, as presently understood, is like *Lacerta* in having a disjunct range with four species in Europe and three in central Africa (viz. *A. africanus*, *A. alleni* and *A. vauereselli*). As with *Lacerta*, the equatorial species have no close affinities with their Palaearctic congeners and must be removed from *Algyroides* (see Appendix I). Both *Algyroides* and *Psammodromus* (four species in northwest Africa and southwest Europe) are usually regarded as being closely related to *Lacerta*. *Algyroides* differs externally from *Lacerta* only in possessing strongly enlarged dorsal scales ; *Psammodromus* also has enlarged dorsal scales but differs from both *Algyroides* and *Lacerta* in having the collar reduced or absent.

This paper consists of four sections : (i) a statement of the present classification (p. 294) ; (ii) a description of the principal characters that have either already been used to classify *Lacerta*, *Algyroides* and *Psammodromus* or that appear to be potentially useful (p. 300) ; (iii) an assessment of the relative importance of these characters (p. 315) and (iv) an attempt to revise the classification (p. 327).

THE PRESENT CLASSIFICATION OF *LACERTA*, *ALGYROIDES* AND *PSAMMODROMUS*

Genus ***LACERTA*** Linnaeus 1758

Until very recently, the subgeneric allocations of forty (almost 80 per cent) of the species of *Lacerta* were widely accepted and these are listed below. The characters on which the subgenera of *Lacerta* are based are set out in Table I (p. 296) together with those of *Algyroides* (Palaearctic forms) and *Psammodromus*.

Subgenus *Lacerta* s. str. Linnaeus 1758 (type species : *L. agilis*)
agilis Linnaeus 1758 (West and central Europe to central Asia), *schreiberi* Bedriaga 1878 (Iberian Peninsula), *strigata* Eichwald 1831 (Caucasus area ; West Iran), *trilineata* Bedriaga 1886 (Southeast Europe and Southwest Asia), *viridis* (Laurenti 1768) (central and southern Europe etc.).

Subgenus *Gallotia* Boulenger 1916 (type species : *L. galloti*)
atlantica Peters & Doria 1882 (eastern Canary Islands), *galloti* Duméril & Bibron 1839 (western Canary Islands, not Gran Canaria), *simonyi* Steindachner 1889 (Gran Canaria, formerly Roques Zalmor off Hierro, western Canary Islands).

Subgenus *Zootoca* Wagler 1830 (type species : *L. vivipara*)
andreanszkyi Werner 1929 (Atlas Mountains), *praticola* Eversmann 1834 (Caucasus and northern Balkan Peninsula), *vivipara* Jaquin 1787 (northern Eurasia).

Subgenus *Podarcis* Wagler 1830 (type species : *L. muralis*)
dugesii Milne-Edwards 1829 (Madeira), *erhardii* Bedriaga 1882 (southern Balkan Peninsula and Greek Islands), *filfolensis* Bedriaga 1876 (Malta and nearby islands), *hispanica* Steindachner 1870 (Iberian Peninsula and Northwest Africa), *lilfordi* (Günther 1874) (Balearic Islands), *melisellensis* Braun 1877 (eastern Adriatic region), *milensis* Bedriaga 1882 (Milos and nearby islands), *muralis* (Laurenti 1768) (South and central Europe), *pityusensis* Boscá 1883 (Ibiza and nearby islands), *sicula* Rafinesque 1810 (mainly Italy, Adriatic and Tyrrhenian areas), *taurica* Pallas 1814 (southeastern Europe), *tiliguerta* Gmelin 1789 (Corsica and Sardinia), *wagleriana* (Gistel 1868) (Sicily).

Subgenus *Archaeolacerta* Mertens 1921 (type species : *L. bedriagae*)
armeniaca Méhely 1909 (Caucasus), *bedriagae* Camerano 1885 (Corsica and Sardinia), *caucasica* Méhely 1909 (Caucasus), *dahli* Darevsky 1957 (Caucasus), *danfordi* (Günther 1876) (western Turkey and south to Petra), *graeca* Bedriaga 1886 (southern Greece), *horvathi* Méhely 1904 (northwestern Jugoslavia), *monticola* Boulenger 1905 (Iberian Peninsula), *mosorensis* Kolombatović 1886 (southwestern Jugoslavia), *oxycephala* Duméril & Bibron 1839 (southwestern Jugoslavia), *rostombekovi* Darevsky 1957 (Caucasus), *rudis* Bedriaga 1886 (Caucasus), *saxicola* Eversmann 1834 (Caucasus etc.), *unisexualis* Darevsky 1966 (Caucasus).

Subgenus *Scelarcis* Fitzinger 1843 (type species : *L. perspicillata*)
perspicillata Duméril & Bibron 1839 (northwestern Africa).

Subgenus *Apathya* Méhely 1907 (type species : *L. cappadocica*)
cappadocica Werner 1902 (central Turkey to northwest Iran).

TABLE I: Characters previously used to distinguish the subgenera of *Lacerta* (*Algyroides* and *Psammodromus* are included for comparison)

	Lacerta s. str.	*Gallotia*	*Zootoca*	*Podarcis*	*Archaeolacerta*
Approximate adult body size (snout–vent)	70–160 mm	60–210+ mm	35–67 mm	45–90 mm	55–85 mm
Skull facies	Massive, deep, roof convex	Massive, deep, roof convex	Fairly light build, roof convex	Moderate-to-light build, roof usually convex	Lightly built, depressed, roof flat
Cranial osteoderms	Thick	Thick	Moderate or thin	Variable	Thin
Supraocular lamellae	Complete	Complete	Complete except in some *L. andreanszkyi*	Usually complete, exceptions in *L. dugesii* and *L. hispanica*	Incomplete in most cases
Pterygoid teeth	Usual	Usual	None	Variable	Almost always none
Micro-ornamentation of hemipenial epithelium (much data from Bohme 1971)	Lobe tips with crown-shaped tubercles. Lobe flanks with long spines, often ending in spinules	Simple, recurved spines	Crown-shaped tubercles but recurved spines in *L. andreanszkyi*	Simple recurved spines (not *L. dugesii*)	Crown-shaped tubercles, except in *L. graeca* and *L. bedriagae*
Postnasal shields	Usually two (one in some *L. agilis*)	One	One	One, in most cases	Variable
Eyelid	Scaly	Scaly	Scaly	Scaly	Scaly
First supratemporal scale emarginates parietal shield	Yes	Varies	Varies	No	Yes, exceptions in *L. bedriagae*
Dorsal scales	Raised, rather imbricate, keeled	Raised and keeled	Raised, often keeled	Usually raised, often keeled	Often flat and unkeeled
Collar	Serrated	Varies	Serrated	Serration usually weak but varies	Unserrated
Ventral scaling: shape of scales	Inclined parallelograms, strongly imbricate	As *Lacerta* s. str. but imbrication weaker	As *Lacerta* s. str., but imbrication weaker	Approximate rectangles, overlap varies	Rectangular, little imbrication
Ventral scaling: number of longitudinal rows	6–8	(8) 10–20	6	6 (8)	6–8
Subdigital tubercles	Normal	Normal	Normal	Normal	Normal
Sexual dimorphism in dorsal pattern	Frequent	Frequent	None or little	Usual	Often none
Tail brightly coloured in the young	No	No	No	In a few populations	Frequently

	Scelarcis	*Apathya*	*Algyroides*	*Psammodromus*
Approximate adult body size (snout–vent)	40–60 mm	50–80 mm	30–70 mm	35–80 mm
Skull facies	Moderate-to-light build, roof often flat	Lightly built, depressed, roof flat	Variable	Moderate-to-heavy build, roof convex
Cranial osteoderms	Fairly thin	Thin	Thin to moderate	Moderate to thick
Supraocular lamellae	Variable	Usually incomplete	Variable	Complete
Pterygoid teeth	None	None	Variable	Variable
Micro-ornamentation of hemipenial epithelium (much data from Böhme 1971)	Simple recurved spines	Simple recurved spines	Variable	Variable
Postnasal shields	Two	Two or three	Usually two	Usually one
Eyelid	Transparent window of one scale	Transparent window of several scales	Scaly	Scaly
First supratemporal scale emarginates parietal shield	No	Not clearly emarginated	Yes	No
Dorsal scales	Not strongly raised, unkeeled	Not strongly raised, unkeeled	Large, imbricate, keeled, often pointed	Large, imbricate, keeled and pointed
Collar	Unserrated	Unserrated	Serration variable	Collar very weak or absent
Ventral scaling: shape of scales	Rectangular, little imbrication	Rectangular, little imbrication	± as *Podarcis*	As *Lacerta* s. str. or overlap even stronger
Ventral scaling: number of longitudinal rows	10	6–8	6	6–10 (see p. 348)
Subdigital tubercles	Normal	Usually strongly keeled	Normal	Normal or keeled
Sexual dimorphism in dorsal pattern	None	None	None, except in *A. moreoticus*	None
Tail brightly coloured in the young	Yes	Yes	No	No

The precise systematic positions of the following eleven species are less certain.

L. lepida Daudin 1802 (southwestern Europe and northwestern Africa)
L. parva Boulenger 1887 (Turkey and Armenia)
L. princeps Blanford 1874 (eastern Turkey to southwestern Iran)

Boulenger (1916) placed these species in the subgenus *Lacerta* s. str., but Peters (1962) believed that they had no close relationship with the other forms in this subgenus. Indeed Peters (1961) put *L. lepida* in the subgenus *Gallotia* and (1962a) suggested that the affinities of *L. parva* lie with *L. fraasii* (q.v.). More recently, Eiselt (1968) has again placed *L. princeps* close to the members of the subgenus *Lacerta* s. str.

L. fraasii Lehrs 1910 (Lebanon)

Boulenger (1920) emphasized the similarity of this species to *L. vivipara* and even thought that the two forms might be conspecific. He consequently placed *L. fraasii* and *L. vivipara* in the subgenus *Zootoca*. Peters (1962a) disputed this close relationship and instead pointed out the likeness between *L. fraasii* and *L. parva* (see above). He suggested that, eventually, a separate subgenus might have to be created for these two species and also discussed their suitability as ancestors of the *Podarcis* group.

L. brandtii De Filippi 1863 (northwestern Iran)

This species was regarded by Boulenger (1920) as " one of the most primitive members of the *L. muralis* group [i.e. *Podarcis* in Boulenger's sense] which it connects with *L. parva* ". Wettstein (1951), on the other hand, believed that *L. brandtii* was connected with *L. vivipara* and *L. fraasii* and allocated it to the subgenus *Zootoca*. Peters (1962) in his discussion of *L. parva* states that the possibility of a relationship with *L. brandtii* should not be dismissed, and Böhme (1971) also believes this.

L. cyanura Arnold 1972 (southeastern Arabia)
L. jayakari Boulenger 1887 (southeastern Arabia)

In his *Monograph of the Lacertidae* (1920) Boulenger placed *L. jayakari* in *Podarcis* as he understood that subgenus, and regarded *L. laevis* as its closest relation. He suggested that both these species might have been derived from ancestral forms close to *L. brandtii*. Klemmer (1957) regarded the position of *Lacerta jayakari* as uncertain. The relationships of this form and the recently discovered *L. cyanura* have been briefly discussed in a recent paper (Arnold 1972).

L. peloponnesiaca Bibron & Bory 1833 (southern Greece)

According to Boulenger (1920) this species is closely related to *L. taurica* which is now placed in *Podarcis* s. str. Klemmer (1957) regarded *L. peloponnesiaca* as *incertae sedis* because it has a very robust skull with heavily ossified temporal areas atypical of the subgenus *Podarcis*. But Buchholz (1960) pointed out that this difference is not clear-cut since the degree of temporal ossification in *L. peloponnesiaca* is very variable.

L. derjugini Nikolsky 1898 (Caucasus)

Méhely (1909) placed *L. derjugini* in his 'Archaeolacertae' and Lantz & Cyrén (1947) followed this allocation, regarding *L. derjugini* as a member of the subgenus *Archaeolacerta.* Other authors list this species as a member of *Zootoca,* e.g. Boulenger (1920), Mertens & Müller (1928, 1940), Klemmer (1957). The last author considered that it might link *Zootoca* with *Archaeolacerta.*

L. chlorogaster Boulenger 1908 (southern Caspian region)
L. laevis Gray 1838 (East Mediterranean coastal region)

Like *L. derjugini* these two species were placed by Méhely (1909) in his 'Archaeolacertae' and most authors have followed this course. However, Mertens (1957) pointed out that *L. chlorogaster* is more like the members of the subgenus *Podarcis* in its skull and body shape and in having keeled dorsal scales and he tentatively transferred it to this subgenus. Similar arguments could be applied to *L. laevis* which resembles *L. chlorogaster* in these respects.

Genus ***ALGYROIDES*** Bibron & Bory 1833 (type species: *A. moreoticus*)

> *fitzingeri* (Wiegmann 1834) (Corsica and Sardinia), *marchi* Valverde 1958 (southeastern Spain), *moreoticus* Bibron & Bory 1833 (southern Greece and Ionian Islands), *A. nigropunctatus* (Duméril & Bibron 1839) (eastern coastal area of Adriatic Sea).

Genus ***PSAMMODROMUS*** Fitzinger 1826 (type species: *P. hispanicus*)

> *P. algirus* (Linnaeus 1758) (southwest Europe and northwest Africa), *blanci* (Lataste 1880) (northwestern Africa), *hispanicus* Fitzinger 1826 (southern France and Iberian Peninsula), *microdactylus* (Boettger 1881) (northwestern Africa).

Recent work

Very recently, Böhme (1971) has challenged certain aspects of the accepted classification of *Lacerta* and its allies on the basis of differences in structure of the hemipenial micro-ornamentation (see p. 309). Amongst his principal findings are the following.

1. *L. lepida* and *L. princeps* appear to be closer to the subgenus *Gallotia* than to *Lacerta* s. str.
2. *Archaeolacerta* may be an unnatural group as two species (*bedriagae* and *graeca*) have a different pattern of micro-ornamentation from the others.
3. *Archaeolacerta* (with the exception of the two species mentioned in paragraph 2) and *Zootoca* are not clearly distinguishable and should be merged.
4. *Psammodromus* and *Algyroides* are probably not natural groups.

CHARACTERS ALREADY USED OR POTENTIALLY USEFUL IN CLASSIFYING *LACERTA*, *ALGYROIDES* AND *PSAMMODROMUS*

In these descriptions, subgeneric names refer only to those species of *Lacerta* definitely assigned on p. 295. Species of uncertain position are mentioned separately.

Osteological characters

1. *General shape of the skull* (Fig. 2)

Most lizards in the genera *Lacerta*, *Algyroides* and *Psammodromus* have a relatively deep, robust skull in which the parietal table has convex lateral edges and is domed in transverse section. But, in contrast, some species of *Lacerta* and *Algyroides* have a flattened, delicately built skull and a parietal table with concave or straight lateral borders and a flat transverse section. Many intermediates exist between these two extremes.

2. *Nasal openings of the skull* (Fig. 2)

In many species the nasal opening is small. It may expose only the external vestibule of the nasal passage but more usually allows the anterior part of the principal nasal chamber to be seen from above. In intact animals it is possible to palpate the nasal opening which in these cases either does not reach backwards under the frontonasal scute or only extends under its anterior borders. In other forms the nasal bones do not extend so far forward and the exposure of the principal nasal chamber is much greater so that the septomaxilla is visible from above. In such cases the openings may extend backwards under the posterior borders of the frontonasal scute or beyond.

3. *Development of cranial osteoderms*

Cranial osteoderms (the *crusta calcarea*) are developed mainly during the period between hatching and maturity and form a continuous layer, closely applied to the dorsal and lateral bones of the skull. They also may develop in previously unossified regions such as the skin over the orbits and in the temporal region. The cranial osteodermal layer is laid down in discrete sections each corresponding to an epidermal scute so that, as the osteoderms increase in thickness, the sutures between the scutes are left as distinct grooves. The development of osteoderms on the skull roof shows a rough correlation with the robustness of the skull; depressed, delicately built skulls have relatively weak osteoderms.

4. *Supraocular lamellae* (Fig. 2)

The dorsal surface of the orbit is unossified in hatchling lizards but eventually is wholly or partly occupied by a series of four osteoderms (the supraocular lamellae) corresponding to the four supraocular scales. These begin to develop near the lateral borders of the frontal bones and slowly extend outwards. In adults of most species the supraocular osteoderms cover the whole orbital area but in a number of forms the second, third and sometimes the fourth osteoderms are usually

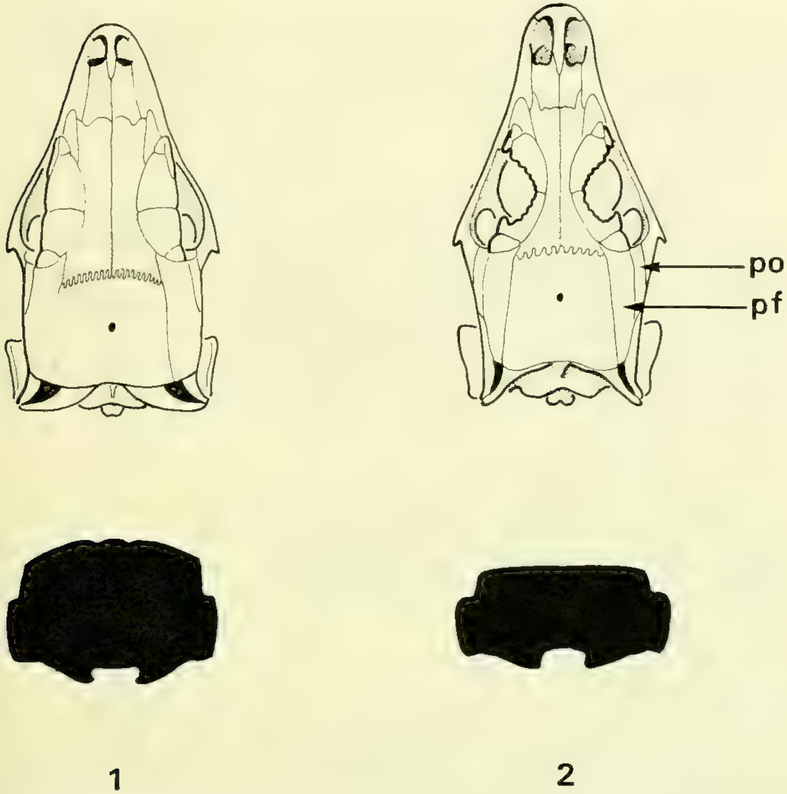

FIG. 2. Principal skull types: dorsal view and cross-profile. (1) Robust undepressed skull with small external nares, complete supraocular lamellae and transversely arched parietal region. (2) Delicately built, strongly flattened skull with large external nares, fenestrated supraocular lamellae and flat parietal region. po = postorbital bone. pf = postfrontal bone.

incomplete so that a flexible area of unossified skin remains between them. This occurs in *Algyroides fitzingeri* and *A. marchi* and in many *Archaeolacerta* spp., in *Lacerta cyanura*, *L.* (*Apathya*) *cappadocica* and some populations of *L.* (*Podarcis*) *hispanica* and *L.* (*Scelarcis*) *perspicillata*, in females of *L.* (*P.*) *dugesii* and in many *L. andreanszkyi*, *L. derjugini* and some *L. fraasii*.

5. *Ossification of the temporal region*

Osteoderms may occur in the skin covering the jaw muscles and bordered by the jugal, postorbital, squamosal and quadrate bones and the lower jaw. Such osteoderms are well developed in adults of most *Lacerta* s. str. species (not *agilis* or some populations of *trilineata*), *L. lepida*, *L. princeps*, *L.* (*G.*) *atlantica*, some

L. (*G.*) *simonyi*, and *L. peloponnesiaca* and in *Psammodromus algirus*. Minor development (particularly along the posterior border of the jugal) may occur in individuals of other species especially in *Podarcis* (commonest in *L. melisellensis* and *L. taurica*).

6. *Pterygoid teeth*

Teeth are found on the pterygoid bones of all species of the subgenera *Lacerta* s. str. and *Gallotia*, in *L. lepida*, *L. princeps*, *L. peloponnesiaca*, *L. brandtii*, *L. jayakari* and *L. laevis*. They also occur in *Psammodromus algirus* and some *Algyroides moreoticus* and *A. nigropunctatus*. Klemmer (1957) has given data for various species in the subgenus *Podarcis*. In this group, some species rarely have pterygoid teeth, in others they occur in a substantial number of individuals and in *L.* (*P.*) *milensis* and *L.* (*P.*) *taurica* they seem to be almost universally present. In *Lacerta* as a whole there appears to be an imperfect correlation between presence of pterygoid teeth and robustness of the skull.

7. *Postfrontal and postorbital bones* (Fig. 2)

These bones are separate in the hatchlings of the majority of *Lacerta* species but fused in the three members of the subgenus *Gallotia*, in *L.* (*Z.*) *vivipara* and in *L. schreiberi*. They are also fused in all four species of *Psammodromus*. In some other forms, these two elements coalesce during life, e.g. *L. lepida*, *L. dugesii* and in old individuals of several other species.

8. *Number of presacral vertebrae*

Presacral vertebral number varies both between species and within them (see Appendix III), the usual range for *Lacerta* being 25 to 29* vertebrae, for *Algyroides* 24 to 28 and for *Psammodromus* 26 to 28. Intraspecific variation includes geographical, sexual and intrasexual differences. In each sex of a given species, most individuals usually have the same number of presacral vertebrae (occasionally two numbers are relatively common), the remainder deviate from this figure by one or occasionally two vertebrae. Typically the total range for each sex of a species is not more than three vertebrae. The commonest presacral vertebral numbers of each sex generally differ, females usually having on average one more vertebra than males (occasionally it is two more) ; 26 and 27 are the commonest figures for males, 27 and 28 for females. The three species assigned to the subgenus *Gallotia* differ from this pattern in showing almost no sexual or individual variation in vertebral number. This condition is rare in the Lacertidae as a whole, occurring elsewhere only in a few species of *Acanthodactylus*. Of the specimens of *Gallotia* examined in this study (viz. 25 *L. atlantica*, 35 *L. galloti* and 27 *L. simonyi*), nearly all had a presacral vertebral count of 26 irrespective of sex. The exceptions were one male *L. galloti* and two female *L. simonyi* all of which had 25 presacral vertebrae.

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* Two out of 32 female *L.* (*L.*) *agilis* examined had 30 vertebrae as did one out of five female *L.* (*Z.*) *praticola*.

9. *Clavicle* (Fig. 3)

Some individuals of *Lacerta, Algyroides* and *Psammodromus* have clavicles that correspond to the condition found in the Lacertidae as a whole. In these the clavicle is greatly expanded near the midline and the expansion is penetrated by a large foramen so that the bone in this region forms a continuous loop (Fig. 3(2)).

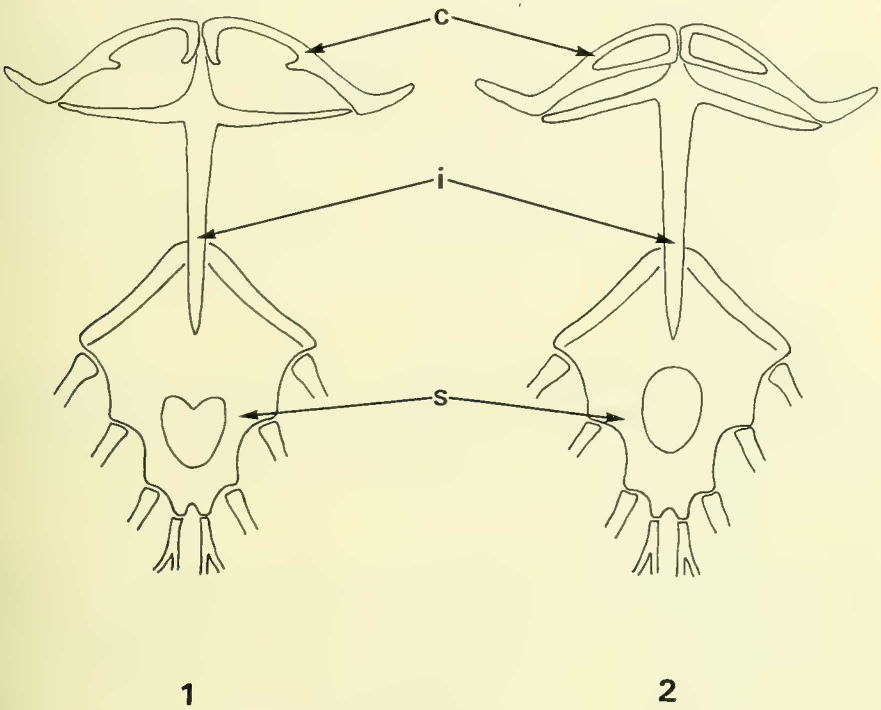

Fig. 3. Variations in clavicle, interclavicle and sternum. (1) Clavicle emarginated, interclavicle with lateral arms approximately at right angles to its longitudinal axis, sternum with heart-shaped fontanelle. (2) Clavicle unemarginated, interclavicle with lateral arms directed backwards, sternum with oval fontanelle. c = clavicle. i = interclavicle. s = sternum.

In other individuals the clavicle is emarginated posteriorly so that the loop is interrupted (Fig. 3(1)). This interruption may be minor or the whole posterior section may be missing. In *Psammodromus*, the species of the subgenus *Gallotia* and perhaps in *L. parva* and *L. fraasii* (the small samples available, 17 and 6 respectively, do not permit certainty) the loop of the clavicle is complete in all specimens. In most other species both the intact and emarginated conditions occur, although the proportion of each varies from species to species. In a few *Lacerta* species only the emarginated condition was observed: these include *L.* (*P.*) *filfolensis*, *L.* (*P.*) *muralis*, *L.* (*A.*) *bedriagae*, *L.* (*A.*) *graeca*, *L.* (*A.*) *oxycephala*, *L.* (*S.*) *perspicillata* and *L. brandtii*.

10. *Sternal fontanelle* (Fig. 3)

In all species of *Lacerta*, *Algyroides* and *Psammodromus* the sternum usually has a distinct fontanelle penetrating its posterior area, although it may be unfenestrated in a few individuals of some species. The shape of the fontanelle is somewhat variable in most species but two main patterns are present. The majority of forms nearly always have an oval or round fontanelle while most members of *Podarcis* and *L. peloponnesiaca* have a heart-shaped (cordiform) one in which there is a well-developed, posteriorly directed process arising from the anterior border. Occasionally this extends right across the fontanelle to join its posterior margin, thus dividing it in two. Some individuals of *L. laevis*, *L. danfordi*, *L. andreanszkyi* and *Algyroides moreoticus* also have a sternal fontanelle which approaches a heart-shape but in these species the posteriorly directed process is not well developed.

11. *Interclavicle* (Fig. 3)

This element is cruciform in all species of *Lacerta*, *Algyroides* and *Psammodromus*. The lateral extensions of the interclavicle generally run at about 90° to the main axis of the bone although they may be directed slightly forwards or more rarely slightly backwards. *L.* (*P.*) *dugesii* and *L.* (*S.*) *perspicillata* differ in having the lateral extensions clearly directed obliquely backwards in all individuals examined.

12. *Pattern of tail vertebrae* (Fig. 4)

The systematic importance of variations in the caudal vertebrae of lizards in general has been discussed by Etheridge (1967). Three main patterns are present in the Lacertidae all of which occur in the genus *Lacerta*. Each begins with a proximal series of non-autotomic vertebrae. The number of bones in this proximal series varies from four to seven, males of any species tending to have a higher average number than females. The highest numbers encountered occur in *L. fraasii*.

Apart from the proximal series, the rest of the tail vertebrae are autotomic and the more anterior of these always bear transverse processes. It is these transverse processes which differentiate the three basic patterns (see Fig. 4).

Pattern A. All vertebrae with transverse processes have a single pair anterior to the autotomic plane.

Pattern B. The more anterior of the vertebrae with transverse processes bear two parallel pairs of which the anterior is longer. One pair lies in front of the autotomic plane, one pair behind. Normally from one to four vertebrae are involved although the number may exceptionally be up to seven. This pattern is restricted to *Lacerta* and the European species of *Algyroides*.

Pattern C. Again the more anterior autotomic vertebrae bear two pairs of transverse processes, one each side of the autotomic plane. The members of the more anterior of these pairs run laterally or occasionally are directed slightly

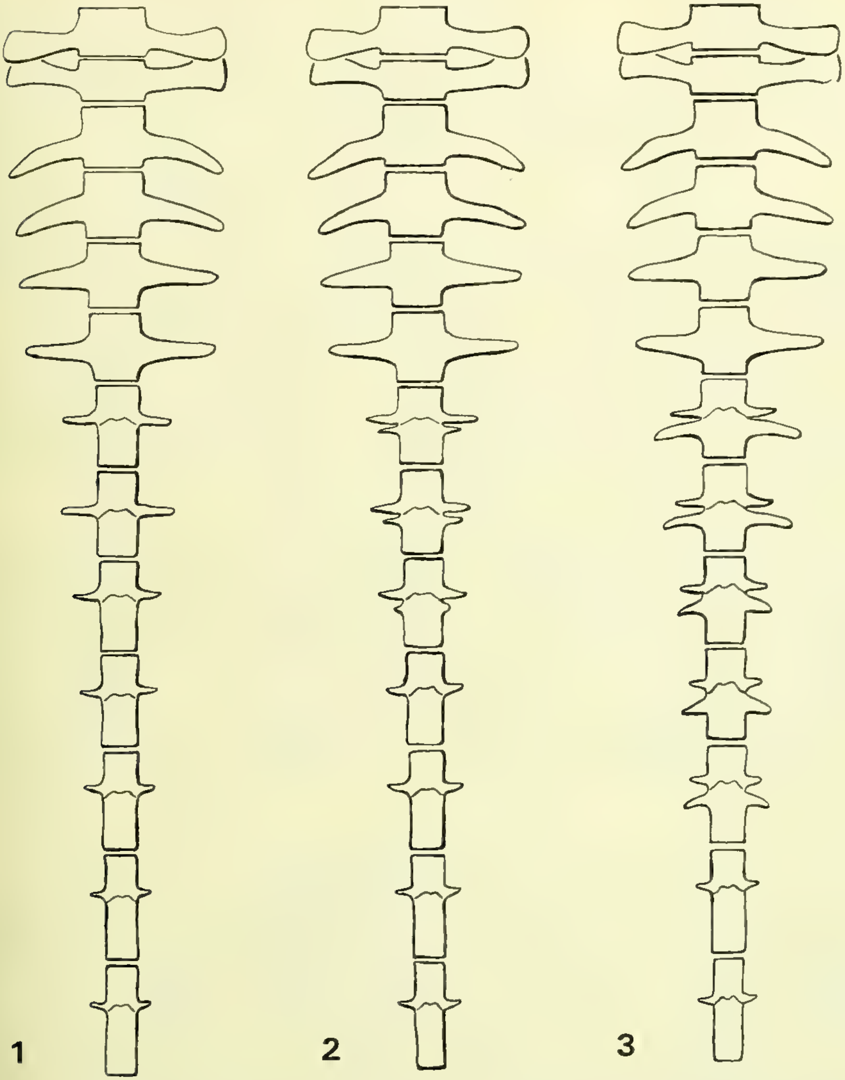

Fig. 4. Principal patterns of caudal vertebrae. (1) Pattern A: vertebrae with single pairs of transverse processes only. (2) Pattern B: some anterior autotomic vertebrae with two, more or less parallel pairs of transverse processes, the posterior pair being the shorter. (3) Pattern C: some anterior autotomic vertebrae with two diverging pairs of transverse processes, the anterior pair being the shorter.

forwards. The members of the posterior pair are often blade-like, usually longer than the front ones, and run obliquely backwards. From three to seven vertebrae are involved.

The A and B patterns are most similar, sometimes differing only in as little as the latter having secondary processes on one vertebra. Furthermore, they frequently occur together in the same population so it seems best to treat them as one class. A or B caudal patterns, or both, are found in all members of *Lacerta* s. str., most *Archaeolacerta*, the species of *Zootoca*, *L.* (*P.*) *dugesii*, *L.* (*S.*) *perspicillata*, *L.* (*Ap.*) *cappadocica*, *L. lepida*, *L. princeps*, *L. jayakari*, *L. cyanura*, *L. derjugini*, *L. laevis* and *L. chlorogaster* ; they are also found in *Algyroides*. The C pattern occurs in all members of *Gallotia*, in most members of *Podarcis* (not *L. dugesii*), in *L. peloponnesiaca*, in *L.* (*A.*) *danfordi* (in the subspecies *L. d. danfordi* and *L. d. anatolica* but not in *L. d. kulzeri*), and in *Psammodromus*.

L. parva, *L. brandtii* and *L. fraasii* have caudal patterns that are, to some extent, intermediate between the B and C types.

L. parva. Two to six vertebrae with double processes (two to four most commonly). The anterior pair is directed somewhat forwards in many individuals while the posterior pair is directed backwards ; in most cases it is larger than the anterior one but it may only be equal to it or even shorter.

L. brandtii. Four to seven vertebrae involved (six being the commonest number). The hind pair of transverse processes diverges backwards as in the C pattern but is usually not longer than the anterior one.

L. fraasii. Number of vertebrae with double processes usually two to four. The posterior pair diverges backwards and may be longer or much shorter than the hind pair.

It has not so far been possible to find any correlation between the caudal pattern and any functional parameter. The pattern does not appear to be related to the type of locomotion adopted or specialized use of the tail or to the ease with which autotomy takes place.

Hemipenial characters

The genitalia of many animals provide useful systematic characters ; for instance the baculum of mammals, the genital armature in insects, various features of the turtle penis (Zug 1966) and the hemipenis of snakes (summarized in Dowling & Savage 1960). Although not generally used, the hemipenes of lizards including lacertids can also provide helpful taxonomic information. Members of a species-group often show a similar hemipenial facies that differs from those occurring in other assemblages. The factors responsible for the evolution of different hemipenial structure in related groups are discussed on p. 324. Differences are not connected with the pattern of copulation for this does not seem to vary much in the Lacertidae. It is unlikely that the differences often function as isolating mechanisms since most sympatric lizard species appear to maintain isolation primarily by ethological means and species most likely to interbreed, that is ones which are closely related, tend to have a similar hemipenial structure.

Technique. In the overwhelming majority of specimens examined, the hemipenes had not been everted before preservation, so the following descriptions are based almost entirely on dissections of retracted organs. The ventral surface of the hemipenis is exposed and one lobe and the stem of the organ are opened by a parasagittal incision. This method of investigation is not entirely satisfactory as it is very difficult to make accurate comparative measurements of the uneverted hemipenis, but a good general impression of the morphology of the organ can be obtained by this means.

General structure of the hemipenis. The hemipenes of all species of *Lacerta, Algyroides* and *Psammodromus* are symmetrically bifurcate with large, usually plicate lobes. The sulcus runs along the hemipenial stem to divide into two branches each of which runs on to one of the lobes. The two lips of the stem sulcus overlap across it, but apically, where each forms the outer lip of one of the lobe sulci, they are usually enlarged and nearly always reflected outwards away from the sulcus. The inner lips of the lobe sulci are typically less developed than the outer ones and are sometimes scarcely apparent especially in the everted organ. However, their degree of development shows some correlation with that of the outer lips.

1. *The armature and the arrangement of the lobes in the retracted organ*

The hemipenes of many lacertid species are apparently different from those of most other lizards in having a clearly defined and often complex supporting structure – *the armature* (Arnold, in press). This is formed of dense connective-tissue and typically consists of a plate-like structure embedded in the dorsal surface of the *retractor magnus* muscle. The plate is attached to the cartilaginous region around the sulcus by a series of short *connectors* and may bear two, often club-shaped bodies, the *clavulae,* which lie between the retracted lobes. In forms where an armature is present, the retracted lobes are not simple sacs as in most other lizards but are flattened and complexly folded. The lobes are also peculiar in that the *retractor magnus* muscle does not insert widely over their surface but only along a narrow tract via a tendinous connexion.

Clearly armatured hemipenes with folded lobes are found in most lacertid genera but not *Takydromus, Platyplacopus, Psammodromus,* the European species of *Algyroides* and most Palaearctic *Lacerta* species. But *L. vivipara* and especially *L. cyanura* and *L. jayakari* have clearly differentiated armatures with distinct folding of the lobes. Armature development is also found in some *L.* (*Ap.*) *cappadocica,* which appear to have traces of lobar folding, and to a lesser extent in *L.* (*A.*) *graeca* where the lobes are not folded at all. Some other species of *Lacerta* have varying amounts of more diffuse connective tissue in the *retractor magnus* muscle and around the hemipenial lobes ; however, it is not differentiated enough to constitute a clear armature although it is almost certainly homologous with this structure. The wide distribution of armatured hemipenes in the *Lacertidae* may indicate that it is the primitive pattern within the family and that the condition found in other species is a secondary simplification. The sporadic occurrence of armatured hemipenes within *Lacerta* tends to support this hypothesis.

2. *Lobe proportions* (Fig. 5)

The hemipenial lobes can each be divided into two parts: an apical section from the apex to the point where the two lobes meet, and the remaining basal section. The relative lengths of these two parts vary although it is difficult to measure them accurately in the retracted hemipenis. The apical section in the majority of species is only about equal to or distinctly shorter than the basal section. In *Podarcis* (excluding *L. dugesii*) the apical portion is nearly always longer than the basal part and may at times be twice as long. This is true also of *Gallotia* (although the two sections may be subequal in *L.* (*G.*) *simonyi*), of *L. peloponnesiaca*, *L.* (*A.*) *danfordi* and to a lesser extent of *L. laevis*. The lobes are long too in *Psammodromus algirus* and in this species they are also rather narrow.

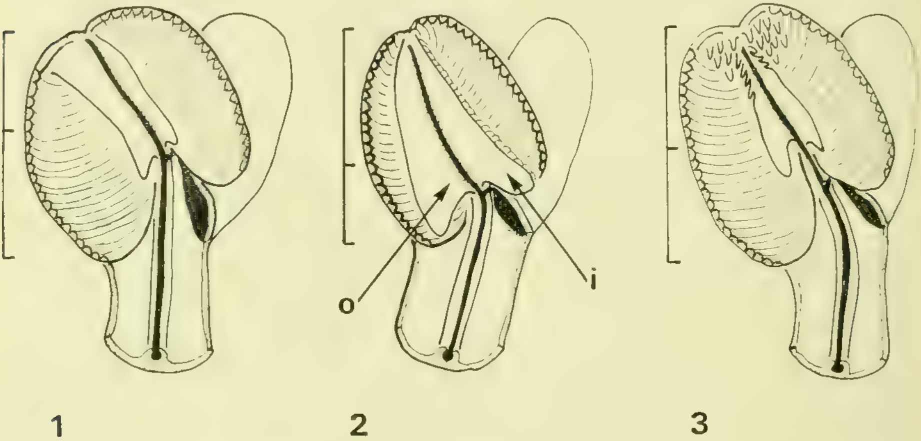

Fig. 5. Variation in hemipenis structure. Diagrams represent retracted organs viewed from below and opened by a parasagittal incision along the stem and one lobe which is spread outwards. Lines at sides indicate relative lengths of apical and basal sections of the lobes. (1) Widespread pattern in *Lacerta*: small sulcal lips, relatively short apical section, no large papillae. (2) Typical pattern in *Podarcis*: large sulcal lips, long apical region, no large papillae. (3) Typical pattern in *Gallotia*: small lips, moderate apical region, long apical papillae. o = outer lip of lobe sulcus. i = inner lip of lobe sulcus.

3. *Size of lips bordering the lobe sulci* (Figs. 5, 6)

The reflected outer sulcal lip varies considerably in size. In most species it is relatively small (Figs. 5(1), 6(1)) but it can be large especially in *Podarcis* (excluding *L. dugesii*). *L. peloponnesiaca* and some *L.* (*A.*) *danfordi* have sulcal lips that are as large as in *Podarcis* and a lesser degree of lip enlargement occurs elsewhere, for instance in *L. laevis*, *L.* (*S.*) *perspicillata* and especially *L.* (*Z.*) *andreanszkyi*. In all these forms the inner lip is also large.

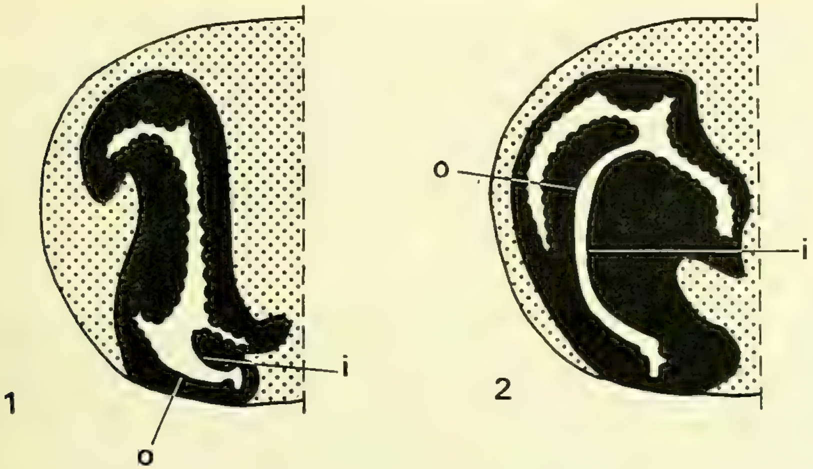

FIG. 6. Variation in hemipenis structure. Diagrams represent transverse sections of single retracted lobes just apical to the hemipenial bifurcation. (1) Small-lipped type (most *Lacerta* spp.). (2) Large-lipped type (*Podarcis*, etc.). o = outer lip. i = inner lip.

4. *Presence of plicae on the lobes*

In *Algyroides, Psammodromus* and nearly all species of *Lacerta*, the lobe surfaces have regular plicae running radially to their apicobasal axes, the only exceptions being *L. fraasii* and *L. parva*. These have the lobe surfaces irregularly folded with a series of longitudinal flaps on them.

5. *Apical papillae* (Fig. 5)

The apical region of each lobe is usually irregularly plicate, although in some members of *Podarcis* there may be a short series of small, blunt tubercles. The three species of *Gallotia* differ from the rest of *Lacerta* in having a terminal lobar area of large, pointed papillae, each of which is conical and somewhat flattened. Relatively large, pointed apical papillae also occur in *Psammodromus blanci, P. hispanicus* and *P. microdactylus*.

6. *Micro-ornamentation of the lobe surface*

Klemmer (1957) pointed out that the minute projections on the lobe plicae differed in shape between various *Lacerta* species and were potentially useful as taxonomic characters. Klemmer based his studies on fresh material (which is inevitably in rather limited supply), but it is possible to examine the pattern of micro-ornamentation in hemipenes extracted from alcohol-preserved specimens, even those over a century old provided they were killed during the mating season, which means that this character can be fairly readily surveyed. Variation in the hemipenial micro-ornamentation of lacertids has recently been studied in some detail by Böhme (1971) and my own observations, using a scanning electron microscope, appear to confirm his.

Basically there seem to be three main types of micro-ornamentation, although intermediates do occur: (1) simple spikes or recurved spines, (2) tubercles with a ring of spinules at their apex (crown-shaped tubercles), (3) irregular, quite often bifurcated tubercles. As will become apparent, closely related species tend to have a similar pattern of micro-ornamentation but there are a number of exceptions to this generalization.

Chromosomes

A review of the rather limited karyological data available for the Lacertidae up to 1968 is given by Gorman (1969). Subsequently Orlova & Orlov (1969), Kupriyanova (1968, 1969) and Gorman *et al.* (1971) have published information on several more species. To date all the genera and species that have been investigated are Palaearctic ones, viz.: *Acanthodactylus*, *Eremias* (subgenera *Eremias* s. str. and *Mesalina*), *Lacerta*, *Ophisops*, *Psammodromus* and *Takydromus*. Nearly all the species examined appear to have the same ' nombre fondamentale ' (i.e. number of chromosome arms, Matthey 1949): in the diploid state this is 38. The commonest diploid formula is 36 acrocentric macrochromosomes plus two microchromosomes. This is found in *Psammodromus algirus*, *P. hispanicus* and the majority of *Lacerta* species investigated, viz. *armeniaca*, *agilis*, *caucasica*, *chlorogaster*, *dahli*, *derjugini*, *laevis*, *lilfordi*, *melisellensis*, *muralis*, *oxycephala*, *praticola*, *rostombekovi*, *rudis*, *saxicola*, *sicula*, *taurica*, *trilineata*, *unisexualis* and *viridis*. *L. lepida*, *L. vivipara* and *L. strigata* deviate slightly from the standard pattern: *L. lepida* has 32 acrocentric macrochromosomes, two metacentric ones and two microchromosomes; *L. vivipara* lacks microchromosomes while *L. strigata* has one of the usual pairs of acrocentric macrochromosomes replaced by a submetacentric pair (Orlova & Orlov 1969). *L. parva*, while exhibiting the standard ' nombre fondamentale ', is peculiar in having only 24 chromosomes in the diploid state: 14 metacentrics and 10 acrocentrics. A more extensive survey of the lacertids might well reveal other variants.

External morphology and colouring

1. *Arrangement of nasal and anterior loreal scales*

The rostral scute and more frequently the first upper labial scute may contribute to the border of the nostril in *Lacerta*, *Algyroides* and *Psammodromus*, but its greater part is made up by scutes usually termed supranasal (lying dorsal, anterior and sometimes ventral to the nostril) and postnasal (lying posterior to the nostril). The scaling in this region occurs in three basic patterns: (1) Supranasal separated from anterior loreal by a single postnasal. (2) Supranasal separated from anterior loreal by two superposed postnasals. (3) Supranasal contacting anterior loreal over a single postnasal. These three patterns usually occur with a single anterior loreal but in some populations of *L.* (*L.*) *agilis* and in *L.* (*Ap.*) *cappadocica* the scaling posterior to the nostril is very variable and there may be either one or two anterior loreals and in *L.* (*Ap.*) *cappadocica* up to three postnasals.

In fact the number of postnasals not infrequently varies within species but sometimes it is relatively stable throughout what, on other grounds, appears to be a natural species-group, e.g. there are two postnasals in most members of the subgenus *Lacerta* s. str. but only one in *Gallotia* and in the majority of individuals of *Podarcis*. Because it is so easily observed, postnasal number can be a useful, although by no means infallible, keying character.

2. *Lower eyelid*

The two monotypic subgenera of *Lacerta*, *Apathya* and *Scelarcis*, are partly based on possession of a distinctly transparent ' window ' in the lower eyelid. In *L.* (*Scelarcis*) *perspicillata* this consists of a single large scale but in *L.* (*Apathya*) *cappadocica* the window is made up of from six to eight smaller elements which have conspicuous dark borders. In fact many small lacertids without eyelid windows appear to be able to see, to some extent, through the lower eyelid which is often translucent enough in living animals for the pupil and iris to be visible when the eye is closed. In a number of species there is a series of enlarged scales in the centre of the eyelid and in *L. dugesii* these are sometimes as large as those found in *L.* (*Ap.*) *cappadocica*. Indeed the principal distinctive eyelid features of this last species are the distribution of pigment (concentrated at the scale edges) and increase in transparency rather than gross structure.

The selective forces promoting the development of eyelid windows and permanent spectacles (in which the upper and lower eyelids are fused) are probably varied. Walls (1934) thought that spectacles protect the eyes from mechanical damage, but Williams & Hecht (1955) suggest that pigmented windows may be important in cutting down the intensity of incident light and point out that many species with eyelid windows keep their eyes shut when basking. Another possibility is that eye closure reduces water loss from the corneal surface. This may be important in small heliothermic species with relatively large eyes which customarily bask in hot sun. The potential total water loss from the corneal surface may be quite large compared with the overall water balance of the animal. For instance, Reichling (1957) suggests that corneal transpiration may account for over 20 per cent of total transpirational loss in *Lacerta agilis* (a fairly small-eyed species) at normal activity temperatures. Keeping an adequate liquid film on the cornea might also present problems in these conditions. Certainly eyelid windows and spectacles are quite widespread in small heliothermic lizards, e.g. *Cabrita, Eremias, Holaspis* and *Ophisops* (Lacertidae), *Gymnophthalmus* (Teiidae), *Platysaurus* (Cordylidae), many skinks and diurnal gekkonids.

3. *Supratemporal scales and their relationship to the parietal scutes* (Fig. 7)

The shape and number of the supratemporal scales are very variable in *Lacerta*. In *Lacerta* s. str., *L. princeps*, *L. lepida*, *L. simonyi* there are usually two (or three) large, relatively deep scales, whereas in *Podarcis* the supratemporals are small,

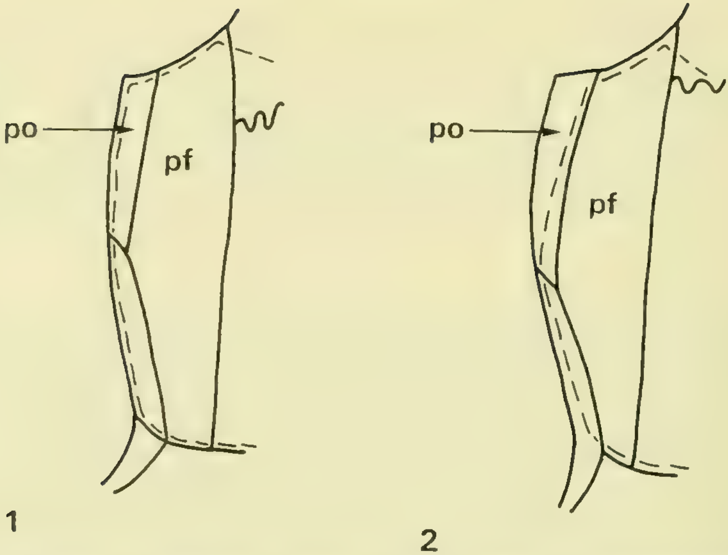

FIG. 7. Differences in relationship between the outer margin of the parietal scale and the underlying bones of the skull. (1) Parietal scale margin running along outer edge of postorbital bone. (2) Parietal scale margin close to postorbital–postfrontal suture. po = postorbital bone. pf = postfrontal bone.

shallow but again of about equal depth. In *L.* (*G.*) *galloti* and *L.* (*G.*) *atlantica*, the anterior supratemporals are much shallower than the posterior ones while in *L.* (*S.*) *perspicillata* and some *Podarcis* the supratemporals are scarcely distinct from the small temporal scaling. Most other species of *Lacerta* and *Algyroides* have a large anterior supratemporal which is both larger and deeper than those following it. In *Psammodromus* the supratemporals may all be about the same depth or there may be some tendency for the anterior ones to be slightly narrowed (*P. algirus*) or enlarged.

Variation in the relationship between the anterior supratemporals and the parietal scute was used by Méhely (1909) to define his two Wall Lizard groups (equivalent to the subgenera *Podarcis* and *Archaeolacerta*). In the former the outer parietal border is usually convex whereas in *Archaeolacerta* it is supposedly emarginated by the first supratemporal. In fact, it is sometimes difficult to decide if the parietal is emarginated and it is often easier in preserved material to see differences in the relationship of the anterior outer border of the parietal to the underlying bones of the skull. In the great majority of *Psammodromus*, *Podarcis*, *L. peloponnesiaca*, *L.* (*S.*) *perspicillata*, *L.* (*Z.*) *andreanszkyi*, *L.* (*Z.*) *vivipara*, *L.* (*G.*) *atlantica* and *L.* (*G.*) *galloti* the anterior border of the parietal scute with the anterior temporal runs along the edge of the skull table (i.e. along the outer edge of the postorbital bone) or very close to it. In the remainder of *Lacerta* (with rare exceptions) and in *Algyroides*, the parietal border either runs along the suture between the postorbital and postfrontal bones (if present) or fairly close to it or alternatively may run forwards from the outer edge of the postorbital to approach the postorbital–postfrontal suture anteriorly.

Méhely (1909) suggested that the peculiar arrangement of supratemporals in *L.* (*G.*) *galloti* and *L.* (*G.*) *atlantica* is a result of the original anterior supratemporals being incorporated into the parietal, the present anterior supratemporals being originally ordinary temporal scales. Some *L.* (*G.*) *galloti* have a cleft in the edge of the parietal in the position where the suture between the first and second supratemporals would be expected to be. Possibly the parietal shields of at least some of the other forms with small apparent supratemporals also incorporate the original supratemporals.

L. (*Ap.*) *cappadocica*, *L. cyanura* and *L. jayakari* are peculiar in having all the supratemporals resting at least partly on the skull table whereas in other species some of the more central supratemporals are off it. *L. jayakari* is also singular in the adults having the posterior supratemporals diagonally elongated so that the anterior part of each lies above the posterior section of the one in front of it.

4. *Dorsal scaling*

Shape. Dorsal scales can be flat or raised, keeled or smooth, juxtaposed or imbricate. In *Lacerta* the dorsal scales are always smaller than the upper caudals but in *Algyroides* and *Psammodromus* they are nearly as large or considerably larger. In these two genera they are also strongly imbricate and keeled and are also often pointed. Scale shape may sometimes correlate with the type of habitat occupied by the species concerned (see p. 320).

Number. The number of dorsal scales in a transverse row at mid-body is a common parameter in lacertid systematics. In *Lacerta* the number varies from as low as 25 in some *L.* (*Z.*) *vivipara* to over 110 in some *L.* (*G.*) *galloti*, and the ranges in *Algyroides* and *Psammodromus* are about 21 to 31 and 15 to 28 respectively. Peters (1961) used the high dorsal count of *L. lepida* compared with its supposed relatives in the subgenus *Lacerta* s. str. as evidence that it should really be placed in *Gallotia* (where two of the three species also have fine scaling). However, there is a trend in *Lacerta* for small species and ones from moist habitats to have lower counts than large forms and ones from more arid regions. As both the fine-scaled members of the subgenus *Gallotia* and *L. lepida* are large and found in quite dry habitats, their high scale numbers might be a result of convergence.

5. *Preanal region*

Most species have a single large preanal scute bordered anteriorly by one or two semicircles of smaller scales. But in some cases the preanal is small or divided and bordered by up to four semicircles of scales. In the preanal region there is again some tendency for the larger species and those from arid regions to have higher numbers of scales.

6. *Collar*

Lacerta and *Algyroides* both have a well-defined collar. That is a backwardly directed transverse skin-fold on the lower surface of the neck, just anterior to the lateral arms of the interclavicle. The outer surface of this fold is covered by a transverse series of large plates. The posterior margins of the plates may form a regular, continuous line (collar smooth) or they may project backwards to form a free serration (collar notched). In *Psammodromus* a collar is either absent or at best very poorly defined.

7. *Ventral scaling*

Shape. There is considerable variation in the shape of the ventral scales and in their degree of overlap among the species of *Lacerta*, *Algyroides* and *Psammodromus*. As with dorsal scaling there is a marked correlation with habitat type (see p. 318).

Number of longitudinal rows. Most species have six longitudinal rows of ventrals but eight is not uncommon, and ten is the usual number in *L.* (*S.*) *perspicillata*, *L. princeps*, *L.* (*G.*) *atlantica*, *Psammodromus algirus* and some populations of *L. lepida*. *L.* (*G.*) *galloti* and *L.* (*G.*) *simonyi* have between 10 and 20 ventral rows.

8. *Keeling on subdigital lamellae*

The subdigital lamellae of nearly all *Lacerta* species are flat or tubercular, but those of the *L.* (*Ap.*) *cappadocica* examined have a single distinct central keel ; *L. cyanura* has a double row of keeled lamellae under each toe and the lamellae of *L. parva* may also occasionally bear two faint ridges (Lantz & Cyrén 1939). This character is sometimes stated or implied to be an adaptation to locomotion on loose surfaces, but its distribution in many families of lizards does not fit this hypothesis since many rock dwelling species also possess keeled lamellae, e.g. *L.* (*Ap.*) *cappadocica*, *L. cyanura*, *Platysaurus* (Cordylidae), various members of *Agama* and *Uromastyx* (Agamidae) and many skinks (e.g. *Mabuya laevis*, *M. quinquetaeniata* and *M. sulcata*). D. Western has made the more likely suggestion (personal communication) that the function of these keels is to reduce the area of contact with hot substrates and thus reduce heat flow. The toes of *Psammodromus hispanicus* are also distinctly bicarinate, while those of *P. microdactylus* and some *P. algirus* are more weakly keeled.

9. *Caudal scale whorls*

One of the characters used by Méhely (1909) to distinguish the subgenus *Archaeolacerta* from *Podarcis* is the degree of variation in the length of the caudal scale whorls. In *Archaeolacerta* the whorls are alternately long and short whereas in *Podarcis* they are said to be subequal. In fact the two conditions are not clearly separated and most members of *Algyroides*, *Psammodromus* and *Lacerta* show at least some alternation in the length of successive scale whorls and proper assessment of this feature thus requires accurate measurement of several whorls on each individual lizard. This makes the character very time-consuming to assess and, as there is also considerable intraspecific variation, it appears to be of rather limited value except as a subsidiary character in identification.

10. *Colour and pattern*

Colour and pattern are very variable in *Lacerta* and to a much lesser extent in *Algyroides* and *Psammodromus* but two aspects in particular seem useful in defining species groups: these are the degree of sexual dimorphism in the dorsal pattern and the presence or absence of bright colour on the belly. Sexual dimorphism in dorsal pattern is well marked in most populations of *Podarcis* and *L. peloponnesiaca* and occurs also in some populations of *Lacerta* s. str. and *Gallotia*. Most other species of *Lacerta* either lack any sexual dimorphism in dorsal pattern or have it only slightly developed. This is also true of *Psammodromus* and most species of *Algyroides* (not *A. moreoticus*).

Bright, often transient ventral colouring occurs in at least some of the breeding individuals of most populations of *Lacerta, Algyroides* and *Psammodromus*. In the majority of these both the throat and belly are brightly coloured and the two areas may contrast with each other. However, in the subgenus *Lacerta* s. str., and in *L. jayakari, L. princeps* and *L. lepida* there is no bright colouring on the belly. This is true also in many populations of *L.* (*P.*) *sicula*, some *L.* (*P.*) *peloponnesiaca* (according to Buchholz 1960) and some *L.* (*P.*) *milensis*. Other individuals of the last species have bright colouring restricted to the second longitudinal rows of ventrals from the mid-line. Breeding males of *Psammodromus algirus* also have a pale belly. Other aspects of coloration are discussed elsewhere.

Hybridization

If two species are able to produce viable (although not necessarily fertile) hybrids, then a relatively close similarity in genetic material and therefore relationship is suggested. A number of cases of hybridization have been reported within *Lacerta* and most of these have been summarized by Mertens (1950, 1956, 1964, 1968, 1972). The various known or assumed crossings are shown diagrammatically in Fig. 8.

It will be seen that in nearly all cases hybridization has been within and not between accepted subgenera. Figure 8(a) involves only members of *Lacerta* s. str.; Fig. 8(b) only members of *Podarcis* and Fig. 8(c) only members of *Archaeolacerta* plus *L. derjugini* which has been assigned to both *Archaeolacerta* and *Zootoca* (see p. 299).

RELATIVE TAXONOMIC VALUE OF CHARACTERS

Introduction

The distribution of many characters customarily used for defining intrageneric groups in *Lacerta* (see Table I) does not always correlate with that of the ‘ new ’ osteological and hemipenial features introduced here, even although the latter tend to correlate well with each other. For instance, it is generally accepted on the

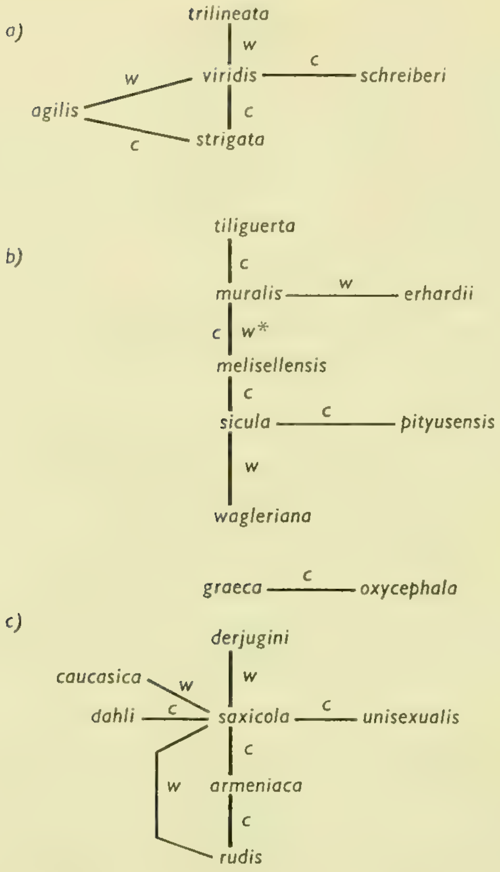
a)
trilineata
w
viridis
c
schreiberi
w
agilis
c
c
strigata
b)
tiliguerta
c
muralis
w
erhardii
c
w*
melisellensis
c
sicula
c
pityusensis
w
wagleriana
graeca
c
oxycephala
c)
derjugini
caucasica
w
w
dahli
c
saxicola
c
unisexualis
c
w
armeniaca
c
rudis

FIG. 8. Known or assumed hybridization between species of *Lacerta*. c indicates hybridization reported from captive animals. w indicates hybridization assumed from morphologically intermediate animals caught in areas of sympatry. * indicates personal observation. For further explanation, *see* text.

evidence of the characters usually employed that *L. dugesii* is a member of the subgenus *Podarcis* but its skeletal and hemipenial characteristics do not support such a relationship. Similarly the lizards now separated into the subgenera *Archaeolacerta*, *Lacerta* s. str. and *Zootoca* are all very similar in many features of their hemipenes and postcranial skeletons which may suggest a closer relationship than is usually acknowledged. This conflict of evidence makes it necessary to assess what relative taxonomic weight should be given to the various characters available. One factor that seems especially important in making this judgement is the comparative lability of the characters concerned. Obviously, beyond certain limits, the more labile a feature is, the less likely it is to indicate real relationships. Among the factors suggesting that a feature is highly labile are the following. (1) High intraspecific variability in a substantial number of the forms under consideration. (2) Continuous variation of the feature throughout the species group being examined (instead of the variation being separable into two or more disjunct character states). This applies specially to characters that involve very simple differences, for instance the relative size or proportions of a morphological feature. These may often be the result of quite small variations in growth pattern and be under polygenic control so that they may be likely to change fairly swiftly in response to selection pressures because there is considerable stored variability in the genotype and fresh mutation is not initially necessary. (3) The suspicion of lability is increased if, especially in the case of a large and varied genus like *Lacerta*, such contrasted characters show a close correlation with environmental parameters. Such correlation may well indicate that a selective pressure connected with the ecological parameter is responsible for the distribution. If the selective pressure and its mode of action in functional terms can be identified, then the case for assuming lability is very strong. Some examples of this sort of character assessment in *Lacerta* are given below.

Ecologically correlated characters

Sympatric species of lizards avoid competing ecologically by utilizing different food resources. But, as the majority of small lacertids are fairly general carnivores and eat whatever small, palatable animals they can overpower, this ecological separation does not usually depend on actively selecting prey species. Where more than one lizard species coexist in precisely the same habitat, separation is usually achieved either by hunting at different periods or by selecting different *sizes* of prey, in which case the coexisting species often differ in size too. But the commonest and most obvious means of dividing resources depends on each species being confined to and exploiting particular areas of the general environment. Spatial separation is common among sympatric species of *Lacerta* and their allies, the division depending on such features as humidity, degree of shade and the physical nature of the lizard's substrate. For instance in some upland areas of southwestern Yugoslavia (at about 1000 m), seven species of *Lacerta* may occur within a few hundred metres of each other. They divide the environment as follows.

Species	*Size*	*Typical habitat*
L. (*A.*) *oxycephala*	Small	Scansorial on sunny rock outcrops, pavements, boulder-screes, etc.
L. (*A.*) *mosorensis*	Small	Scansorial on moister and more shady rock areas than *oxycephala*
L. (*P.*) *muralis*	Small	Less scansorial than *oxycephala* and *mosorensis* but climbs frequently on the base of rock outcrops, on steep earth banks and on vegetated field walls and screes

Species	*Size*	*Typical habitat*
L. (*P.*) *melisellensis*	Small	Largely ground-dwelling in dry places, especially on broken terrain often with some vegetation. Rarely climbs on rocks, etc. but may occasionally climb small bushes
L. (*L.*) *viridis*	Large	In and around bushes especially brambles
L. (*L.*) *agilis*	Medium	Ground-dwelling in dry pastures often with small bushes
L. (*Z.*) *vivipara*	Small	Ground-dwelling in moist well-vegetated places often near water

It is with such differences in spatial niche that many of the characters used in defining *Algyroides*, *Psammodromus* and the subgenera of *Lacerta* can be correlated. Furthermore, they can often be interpreted as functional adaptations to survival in these niches.

Ventral scaling (Fig. 9)

Variation in ventral scaling provides an example of this type of correlation. There are two extreme conditions found in *Lacerta* which are illustrated in Fig. 9: (1) belly scales shaped like inclined parallelograms with the posterior and lateral edges strongly overlapping; (2) belly scales almost rectangular with little or no overlap. Many intermediates between these two conditions also occur. The most complete development of the first condition is found in the large lizards which make up the subgenus *Lacerta* s. str., and in *L. princeps* and *L. lepida*. It exists in a less extreme form in the following smaller species: *L.* (*Z.*) *vivipara*, *L. praticola*, *L. derjugini*, *L. parva*, *L. fraasii* and some species of the subgenus *Podarcis* also tend towards this condition (e.g. *L. taurica*). All these forms are largely ground dwelling in at least partly vegetated areas. If they climb, it is usually in scrub and bushes rather than on open surfaces. An even greater degree of ventral scale imbrication is found in *Psammodromus algirus* which often occurs in and around dense spiny vegetation. The second condition is best developed in the subgenus *Archaeolacerta*, *L.* (*S.*) *perspicillata*, *L.* (*Ap.*) *cappadocica* and in some *Podarcis* (populations of *L. hispanica* and *L. muralis*). In contrast to species having the first condition, these are largely scansorial and most of them climb principally on rock faces, boulders or walls but rarely in bushes.

The two conditions can be 'explained' in functional terms. A ground-living *Lacerta* carries its viscera close to the substrate from which they are separated only by a thin body-wall. When travelling at speed, there is a considerable danger that this wall will be pierced by sharp twigs, dry grass stems or thorns pointing backwards against the direction of motion. Similar risks are faced by lizards in dense bushes. The ventral plates provide protection from such damage, having a hard, mainly β-keratin epidermis (Maderson 1964) and a tough dermal layer. However, these plates are quite rigid and, to permit the sinusoidal movements occurring in locomotion, there are transverse 'hinge' regions housing flexible areas that allow expansion or contraction. Flexible (but non-expanding) hinges

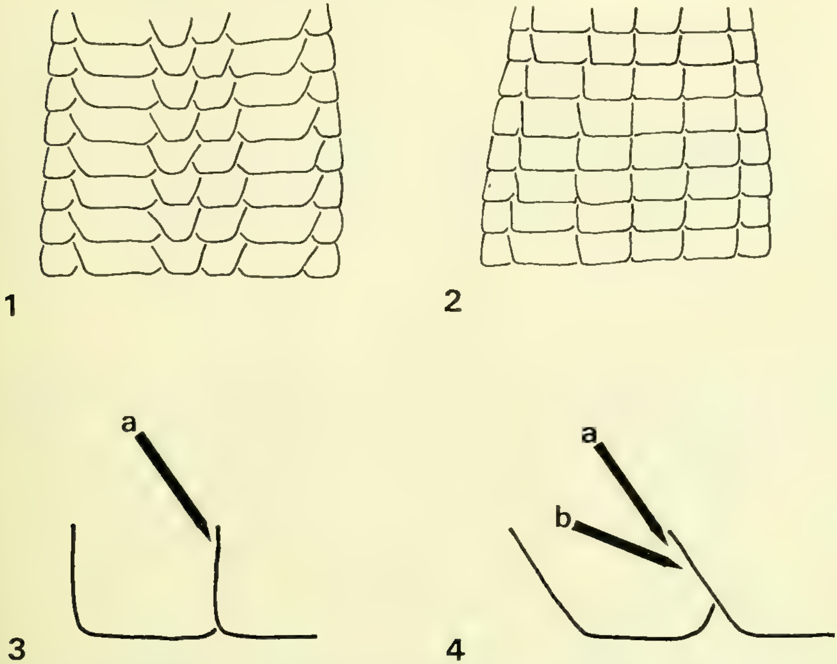

FIG. 9. Ventral scaling. (1) Strongly imbricate, most scales shaped roughly inclined like parallelograms. (2) Little imbrication, individual scales almost rectangular. (3) and (4) *see* text.

run in longitudinal series between the plates and facilitate the movements connected with respiration, lateral and dorsal compression of the body, etc. To provide the necessary flexibility these hinge regions have a thinner, less rigid epidermis largely made up of α-keratin (Maderson 1964) and a thinner dermal layer; they consequently remain likely sites of penetration. (This can easily be confirmed on preserved material with a dissecting needle.) However, the transverse hinge regions are protected by the posterior overlap of each scale and are only exposed if the body is sharply flexed to one side. The roughly longitudinal hinge regions are also protected by imbrication but the protection is increased by the lateral scale margins being oblique. If these margins were parallel to the mid-line of the belly it would be possible for even slightly obliquely directed projections to penetrate under the overlap as in Fig. 9(3). The risk of damage is greatest with projections having axes approaching although not lying on a line parallel to the mid-line (Fig. 9(3a, 4a)), for at more oblique angles (Fig. 9(4b)) it is more likely that the projections will be deflected rather than penetrating. Therefore, by having the scale margins oblique, the risk of a projection entering a hinge is limited to the potentially less damaging ones. All other things being equal, risk of damage by rigid projections increases with increase in size (since the mass and momentum of a lizard tends to increase with the cube of its linear dimensions, including skin thickness). It is therefore not unexpected that the system of overlaps should be better developed in the larger species.

Lizards habitually climbing on rock-faces are much less likely to be damaged by sharp projections and so can usually ' afford ' to do without these elaborate overlaps and their ventral scales themselves are not so resistant to penetration. (Rock-dwelling species of *Lacerta* if accidentally driven into thorn bushes during collection will sometimes get transfixed.)

Collar (Fig. 10)

When present, the collar provides an area of extension allowing movement of the gular skin during head raising. Thus when the head is thrown upwards, the collar fold is pulled out and the soft skin protected by the collar plates is extended (see Fig. 10(A), 10(B)). The various modifications of the collar that occur in *Lacerta* and related genera can, like belly scales, be interpreted as adaptations to particular structural environments. Collars with small, even-edged, only slightly imbricate plates that expose the vulnerable soft skin widely are, as might be expected, confined to habitats with few projections. In more spiky biotopes, there is a tendency for the collar plates to extend backwards to form a denticulate frill giving better protection to the soft skin (e.g. in *Lacerta* s. str.). There is also a trend in such habitats for the sites of expansion not to be confined to a single vulnerable collar area but to be dispersed between a number of transverse rows of gular scales, which in the species concerned are strongly imbricate and thus cover the areas of expansion even when the skin is extended. In the most extreme cases, the collar disappears altogether (e.g. *Psammodromus algirus*), see Fig. 10(C), 10(D).

Dorsal scaling

Dorsal scales show trends in relation to habitat structure that are similar to those found in ventral scaling. Thus species in open environments tend to have small, rather convex scales with little overlap while forms living in biotopes with many projections tend to have larger, more strongly built scales with greater imbrication so that the more vulnerable interstitial skin is better protected. This process reaches its greatest development in *Psammodromus*.

Characters distinguishing the subgenus Archaeolacerta

Many of the features distinguishing the members of the subgenus *Archaeolacerta* (and *Scelarcis* and *Apathya* as well) from the rest of *Lacerta* can be interpreted as functional adaptations to the kind of spatial niche that they inhabit. As stated on p. 318, all the species assigned to *Archaeolacerta*, *L.* (*S.*) *perspicillata* and *L.* (*Ap.*) *cappadocica* are essentially rock-dwelling. (Evidence: *L. graeca*, *horvathi*, *monticola*, *mosorensis*, *oxycephala* – personal observation ; *L. bedriagae* – Lambert 1967 ; *L. danfordi* – Wettstein 1967, M. R. K. Lambert, personal communication ;

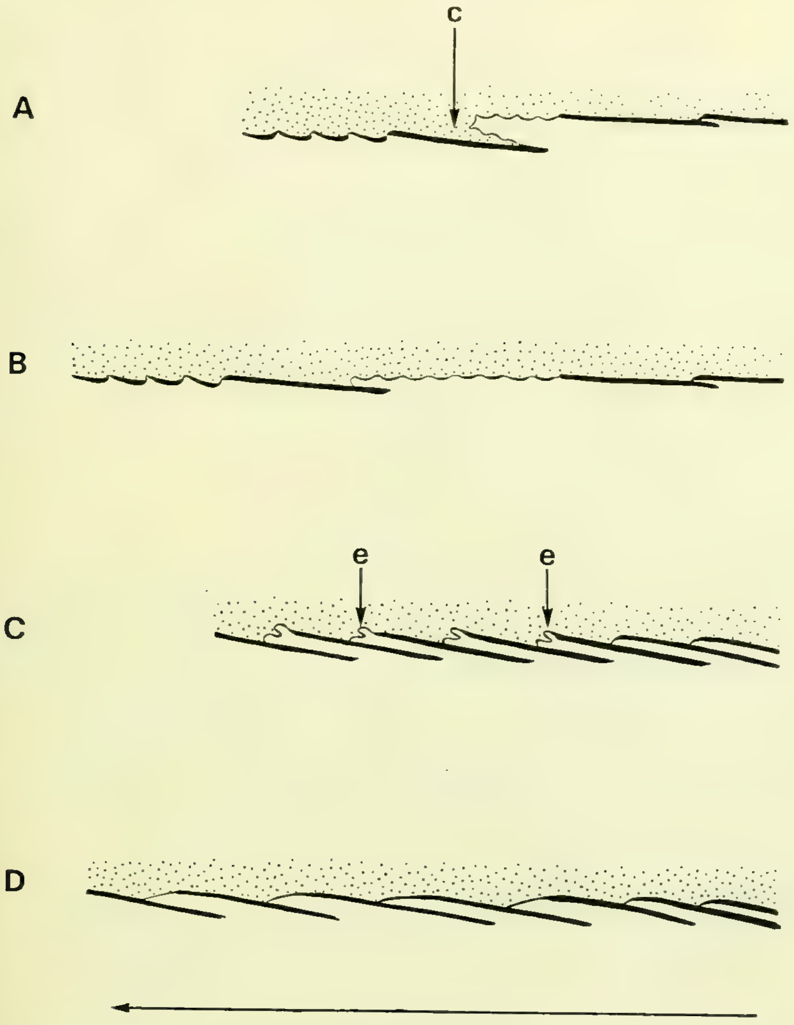

FIG. 10. Different ways of providing elasticity in the gular skin. A and B: restricted area of extensible skin protected by a collar (e.g. in rock-dwelling species of *Lacerta*); A – skin at rest; B – skin stretched. C and D: no collar, extensible skin distributed between a number of overlapping transverse gular scale rows; C – skin at rest; D – skin stretched. c = collar. e = regions of extensible skin.

L. saxicola and other Caucasian forms – Darevsky 1966; *L. perspicillata* – Doumergue 1901; *L. cappadocica* – Reed & Marx 1959, Bird 1936, I. Nader, personal communication.) A more detailed account of adaptations to rock-living in *Lacerta* will be published elsewhere; the following remarks are abstracted from this. Typical *Archaeolacerta* characters are printed in italics.

As with many lizards living in open environments, saxicolous lacertids appear to be subjected to quite severe predator pressure, both from snakes and from birds (shrikes, hawks, etc.). The principal means of avoiding such predators is for the lizards to retreat deep into the narrow frost or sun-induced crevices characteristic of many rock formations and to attach themselves firmly with their claws and by flexing their bodies against the crevice surfaces. Birds cannot follow lizards into such crevices and snakes have difficulty in obtaining enough purchase to extract them. Many *Archaeolacerta* features are connected with this behaviour. The *depressed body* and *low skull* make entrance into very narrow crevices possible. The *weak ossification of the skull* with its *thin flat roof*, *poorly developed osteoderms* and *large nasal openings* gives it a measure of flexibility so that the head can be distorted and wedged into quite irregular fissures. The *flat*, *non-imbricate dorsal scales*, *the narrow collar* and *non-overlapping ventral scutes* allow these lizards to move as easily backwards as forwards in restricted spaces. This is advantageous since backing out of refuges is often necessary.

Depression of the head has secondary effects, one of which involves the eyes. An animal that depends on sight to detect prey and predators cannot 'afford' to reduce the absolute size of its eyes, consequently in lizards with depressed heads these project well above the level of the skull roof. But when such a lizard enters a crevice the eyes must be accommodated within the reduced vertical dimensions of the head. This is accomplished by some of the orbital contents passing downwards through the *suborbital foramen which is enlarged*, so that they project into the buccal cavity. These movements require a much greater flexibility of the supraorbital region and this is provided by the *limited ossification of the supraocular plates*.

The characteristic features of rock-living *Lacerta* species often allow these lizards to avoid predators but paradoxically make their plight worse if they cannot reach a suitable crevice. The fragile skull is easily smashed and the absence of scale overlaps and mechanically strong, raised scales means that the skin is more liable to damage. Furthermore, the lowering of the skull results in the efficiency and size of the jaw muscles being reduced so that specialized rock lizards are less able to actively defend themselves than other species of similar size. There is consequently great advantage in directing attack away from the body towards the more expendable tail. There are often behavioural mechanisms to do this, for instance some rock lizards switch the tail vigorously from side to side when attacked. Also while the body is usually more or less procryptically marked, the *tail in many young rock lizards is blue or green* and conspicuous at close quarters. In the most specialized rock lacertas, e.g. *L. oxycephala*, *L. perspicillata*, *L. cappadocica*, *L. cyanura*, this colouring may be retained by adults too. Furthermore, the tails of rock lizards appear to be more easily autotomized than those of other forms (well over 90 per cent of adults in some populations of *L. oxycephala* have regenerated tails).

Evolution of low autotomy thresholds is probably facilitated by the tail being of less locomotory importance in scansorial lizards than in ground dwelling ones. Y. Werner (1968) has demonstrated a similar correlation between habitat and rate of autotomy in geckoes.

Many of the characters typical of rock-dwelling lacertas also occur in saxicolous species of other families, e.g. *Afroedura, Ptyodactylus* and *Quedenfeldtia* (Gekkonidae) ; *Oplurus, Sauromalus, Petrosaurus* (Iguanidae) ; some *Xantusia* (Xantusiidae) ; *Mabuya sulcata, M. laevis* (Scincidae) ; *Platysaurus* (Cordylidae).

The correlation between the development of this syndrome of characters and rock-dwelling is often quite precise. Thus *L. monticola cyreni* appears to be less strictly restricted to rocks and crevices than the three Yugoslav species of *Archaeolacerta* (*L. horvathi, L. mosorensis* and *L. oxycephala*) and has the characteristic saxicole features less well developed than in these species. Similarly although most species of *Podarcis* climb to some extent, only some populations of *L. hispanica* seem to be almost exclusively rock-dwelling. These are the only members of the subgenus to show very distinct development of features supposedly characteristic of *Archaeolacerta*, etc.

Discussion

Thus the distribution of many of the characters traditionally used in the systematics of *Lacerta* and allied genera can at least be tentatively related to ecological parameters and often to particular strong selective pressures. This suggests that they are rather labile, a conclusion supported by many of them being continuously variable throughout the group, in some cases by their showing some intraspecific variability and by the fact that differences between contrasted characters are often the result of quite small changes in growth pattern. For example, the supraocular pattern shows two characteristic adult states, viz. ' supraocular bones complete ' and ' supraocular bones fenestrated ' which both develop in ontogeny from an unossified juvenile condition. In most species the osteoderms develop fast, spreading outwards from the border of the frontal until the whole supraocular area is covered, but in *Archaeolacerta* and other rock species the process is much slower so that by maturity there is still an unossified (i.e. fenestrated) area. That this state is merely the result of a comparative retardation in growth rate is indicated by the occurrence of complete osteoderms in old specimens of some *Archaeolacerta* species (Klemmer 1957).

The apparent lability of the characters discussed above suggests that they should be given relatively low weight in assessing relationships although it could of course be argued that the other characters available for classifying *Lacerta* and its allies are just as likely to be labile and that this is not recognized because the selective factors responsible for their lability are unknown. This is true, but provided the possibility of high lability has been carefully considered for all features, it seems better in cases where two sets of characters suggest different classifications, to base systematic decisions on the set not known to be potentially or actually very labile. Of course, low lability does not imply that characters are non-adaptive. There are many situations where a character may be fairly stable, yet of great functional significance.

In some cases, the contrasted characters, or systems to which they contribute, may represent different solutions to a particular problem, which are superior, in most circumstances, to intermediate conditions. They may be integral parts of complex functional systems that are unlikely to be interconvertible without dissolution of the system concerned. Thus rock lizards have different means of protecting the eyes when they enter crevices. One of these, where part of the orbital contents passes through a large suborbital foramen has already been described (p. 322). Cordylids (*Platysaurus*) use another: the suborbital foramen being small, part of the orbital contents is passed into the interpterygoid vacuity. Presumably once a rock lizard is committed to one of these methods it could not change to the other without a period of greatly reduced efficiency. Contrasted characters may represent solutions to a particular problem unconnected with the specific requirements of different niche-types. For example, Cryptodire and Pleurodire chelonians both protect the head by withdrawing it into the shell but they employ quite different means of folding the neck. Again it seems likely that the two methods are not interconvertible and the anatomical modifications connected with these methods thus make very good characters for defining the two groups. The various types of adhesive pad found on the toes of geckoes are a similar case (A. P. Russell, personal communication). While it is not yet possible to explain the stability of the lacertid characters discussed here in this way, analogous reasons for low variability seem possible.

Among the features of *Lacerta* and its allies that seem to be generally quite stable intraspecifically and for which there are no obvious external grounds for regarding as particularly labile are the following (although in the present context, stable and labile are purely relative terms since, among the species under consideration, most characters are subject to occasional exception): postorbital - postfrontal fusion, sexually correlated variation in vertebral number, shape of the sternal foramen, caudal vertebral pattern, position of the lateral border of the parietal shield and various aspects of hemipenial structure. There are additional reasons for considering the latter to often be good indicators of relationship and these are discussed below.

Hemipenial characters

As already stated, genital characters have often been found pragmatically to be sensitive indicators of relationship (although like any other character source they are not infallible). In the lacertids, the differences between hemipenial types do not appear to be related to differing methods of copulation, or often to be isolating mechanisms. Nor is it possible at present to relate them to particular environmental selection pressures, either acting directly on the hemipenis or indirectly by producing modification of some other part of the animal which in turn causes selection to alter the form of the hemipenis itself.

Mayr (1970) suggests that genital differences might often be pleiotropic by-products of changes in the genotype induced by selection acting on other parts of the animal. This may well be so but does not entirely explain why genitals are often such particularly good indicators of relationship. The reason may be as follows. With most organ systems, any pleiotropically induced change is likely to result in a lowering of functional efficiency. However, provided this reduction in efficiency does not outweigh the original selective advantage of the genetic change concerned, the pleiotropic alteration will initially become fixed. But there will then be normalizing selection modifying the genotype further so that the pleiotropic changes will tend to be suppressed and the organ will return towards its original state and level of efficiency ; see Fig. 11(a).

One would expect rather similar events to take place when pleiotropic changes occur in the genitals but the process will not be exactly the same, since the efficiency of these organs cannot be considered in isolation but only in relation to their co-ordinated functioning with the genitals of the opposite sex which are also under selective control. (Presumably copulatory efficiency depends largely on a good physical match of the genitals rather than their absolute size and shape.)

Consequently, if there is a pleiotropic change in the male organs which reduces copulatory efficiency in some way, there will not only be normalizing selection acting on the male genotype to bring the male organ back towards its original condition, but also, simultaneously, selection acting on the female genotype to produce changes in the genitals compensating for, and adapting to, the pleiotropic alterations that have already taken place in the male system. This means that the two sets of genitals may return to their previous efficiency without reverting to their original morphological state ; see Fig. 11(b). Presumably the converse situation also exists where pleiotropic changes in the female system produce compensatory alteration in the male.

The genitals are thus likely to ' store ' pleiotropic changes which in other organ systems would probably be eradicated. Furthermore, the genitals of each sex will tend to be altered not only by direct pleiotropic effects on themselves but also by those causing changes in the genitals of the opposite sex. It would consequently be expected that differences in hemipenial structure would often bear some relation to the overall genetic differences between the species compared.

Genitals, at least in lizards, are often good indicators of relationship partly because they alter in the way described above but also because their rate of change is not too fast, so that closely related forms tend to retain quite similar structural patterns. One possible reason for this is that the original extent of pleiotropic changes is reduced by compensating selection in the opposite sex.

Another possible explanation of hemipenial variability is that the female genital system in lizards is much more flexible and much less precisely structured than the hemipenis and could perhaps therefore often accommodate itself immediately, without genetic change, to slight pleiotropic alterations in the hemipenis. This would mean that such minor pleiotropic changes in the male organ would not be subject to normalizing selection or the rather more complex process described above. But if this was generally so, one would expect greater intraspecific variation than

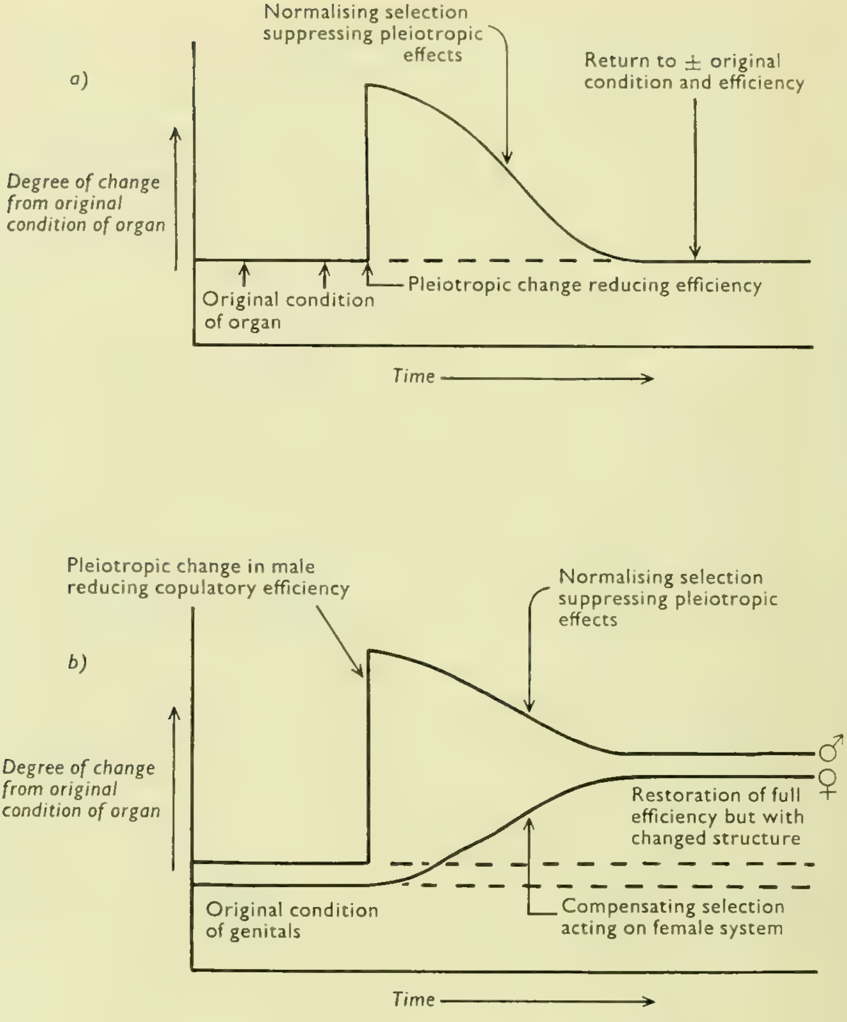
a)
Normalising selection suppressing pleiotropic effects
Return to ± original condition and efficiency
Degree of change from original condition of organ
Original condition of organ
Pleiotropic change reducing efficiency
Time
b)
Pleiotropic change in male reducing copulatory efficiency
Normalising selection suppressing pleiotropic effects
Degree of change from original condition of organ
♂
♀
Restoration of full efficiency but with changed structure
Original condition of genitals
Compensating selection acting on female system
Time

FIG. 11. For explanation *see* text.

has so far been encountered in lizard hemipenes. However, this factor may have some effect.

Although there are reasons for believing that hemipenial characters may frequently be particularly good indicators of relationship, they are not infallible pointers and must be treated with as much caution as any other type of character. For it is quite probable that they are altered by direct environmental selective pressure on occasion. Also, as the overall form of the hemipenis is relatively simple, one must sometimes expect parallel development of similar structure in forms which are not particularly closely related, especially at the lower taxonomic levels.

Böhme (1971) has placed considerable emphasis on hemipenial micro-ornamentation as an indicator of relationship (see p. 299). However, when all available characters including other hemipenial features are taken into consideration, it appears that although hemipenial micro-ornamentation is usually similar in closely related species there are exceptions and the character consequently does not always indicate natural groupings.

RECLASSIFICATION OF *LACERTA, ALGYROIDES* AND *PSAMMODROMUS*

If the species of *Lacerta, Algyroides* and *Psammodromus* are arranged on the basis of those features listed on p. 324 as seeming relatively stable, it is found that there are a number of clearly defined species-groups, the members of each having more or less the same combination of these characters. Furthermore, some other features of less certain relative stability correlate quite well with this arrangement thus providing additional evidence that the groups are natural ones, e.g. number of postnasal scales, degree of sexual dimorphism, scale size, etc. The principal characters of the species-groups are listed in Table II.

Algyroides (excluding the African species) and *Psammodromus* appear to be natural assemblages while Palaearctic *Lacerta* can be divided into four main groups. The principal features of these taxa are given in Table II, p. 328. The *Lacerta* groupings are as follows.

1. Equivalent to the subgenus *Lacerta* s. str. including *L. princeps* and *L. lepida*.
2. Including the subgenera *Zootoca*, *Archaeolacerta*, *Scelarcis* and *Apathya* plus all species not included in other groupings.
3. Members of the subgenus *Podarcis* excepting *L. dugesii* which is placed in group 2 ; and *L. peloponnesiaca*.
4. Equivalent to the subgenus *Gallotia*.

As defined here, groups 1, 3 and 4 are relatively homogeneous while group 2 is much more varied and is in fact a polythetic assemblage. Groups 3 and 4 are quite distinct, both from each other and from groups 1 and 2 which in contrast are generally quite similar. In the interests of nomenclatorial stability it would be desirable, if possible, to retain *Lacerta* more or less as it is presently understood and recognize the groupings within it at an intrageneric level. However, this cannot easily be done for two of the groups have greater affinities with other genera than they do with the rest of *Lacerta*. Thus group 4 seems to be more nearly related to *Psammodromus* than to the other *Lacerta* groupings. Similarly there is a much closer relationship between group 2 and *Algyroides* than between groups 2 and 4 or groups 3 and 4. *Lacerta*, as it stands, is therefore a rather artificial assemblage and it seems best to divide it to produce more homogeneous entities. The most convenient way of doing this is to leave the very similar groups 1 and 2 in *Lacerta* and raise the other two groupings to the rank of full genera, group 3 becoming *Podarcis*

TABLE II : Principal features of *Algyroides*, four proposed taxa originally included in *Lacerta*, and *Psammodromus*

	Algyroides	*Lacerta*				*Psammodromus*
Proposed classification	*Algyroides*	Group 1 *Lacerta* Part I	Group 2 *Lacerta* Part II	Group 3 *Podarcis*	Group 4 *Gallotia*	*Psammodromus*
Number of species	$n = 4$	$n = 7$	$n = 28$	$n = 13$	$n = 3$	$n = 4$
Osteology						
Postorbital and postfrontal bones separate at least in young	+	+ (exception)	+ (exception)	+	−	−
Sex-correlated variation in presacral vertebral no. present	+	+	+	+	−	+
Clavicle emarginated in some individuals of all or most species	+	+	+	+	−	−
Sternal fontanelle oval, not heart-shaped	+ (partial exception)	+	+ (partial exceptions)	− (in most cases)	+	+
Caudal vertebrae pattern A or pattern B	+	+	+ (exceptions)	−	−	−
Hemipenial features						
Apical portion of hemipenial lobes long	−	−	− (exceptions)	+	+ or intermediate	+/−
Lips of lobe sulci large	−	−	− (exceptions)	+	−	+/−
Long, conical papillae on lobe tips	−	−	−	−	+	+/−
Micro-ornamentation of crown-shaped tubercles	+/−	+/−	+/−	−	−	+/−

External features						
Usually two postnasals	+	+ (exceptions)	+/−	−	−	−
Parietal shield reaches outer edge of postorbital bone anteriorly	−	−	− (exceptions)	+	+/−	+
Dorsal scales relatively large	+	− (fairly large in one species)	−	−	− (fairly large in one species)	+
Collar present	+	+	+	+	+	− (or weak)
Number of longitudinal ventral scale rows	6	6–10	6–10	6 (8)	(8) 10–20	6, 10
Sexual dimorphism in dorsal pattern	− (exception)	+ (exceptions)	− (exceptions)	+ (few exceptions)	+	−
Belly brightly coloured in breeding males	+	−	+ (exception)	+ (exceptions)	+	+ (exception)
Adult size large (often over 100 mm snout to vent)	−	+ (exception)	− (exception)	−	+/−	−

and group 4 *Gallotia*. This would produce genera with roughly the same degree of difference that is found in other parts of the Lacertidae. Such a course will result in new name combinations for the sixteen members of groups 3 and 4. This is unfortunate but probably will not cause much confusion as the new generic names have already been widely used as subgenera. An alternative course would have been to include both European *Algyroides* and *Psammodromus* in *Lacerta*, but this would also necessitate some name changes and would result in a large and very varied genus difficult to diagnose adequately.

LACERTA Linnaeus

Linnaeus, 1758, *Syst. Nat.*, ed. 10, vol. **1** : 200.

TYPE SPECIES : *Lacerta agilis* Linnaeus.

DIAGNOSIS. Small to very large lacertids (from 35 mm to over 210 mm snout to vent). Skull shape variable, parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones separate in young of most species but sometimes fuse during life ; clavicle strongly expanded medially, foramen either emarginated or not (the two conditions often existing within the same population) ; interclavicle cruciform, the lateral arms not strongly directed forwards ; sternal fontanelle almost invariably present, nearly always roughly oval ; sexual variation in presacral vertebral number present ; all presacral vertebrae with ribs, except the first three cervicals ; free ribs divided into two series – an anterior one of long ribs and a posterior one of short ribs ; caudal vertebrae typically of A or B pattern (rarely C). Hemipenes symmetrically bilobed. Typically armature absent and lobes not complexly folded (there are exceptions) ; lobes usually plicate, micro-ornamentation variable ; apical regions of the lobes usually short (exceptions) with small sulcal lips (exceptions) ; no large conical papillae at lobe tips. Head shields normal ; nostril usually in contact or close to the first upper labial scute, bordered posteriorly by one, two or rarely three postnasals ; lower eyelid usually scaly although a small transparent window may be present ; anteriorly parietals typically do not extend to outer margin of postorbital bone, first supratemporal scale often large ; masseteric shield often present.

Dorsal body-scales small or moderate (smaller than proximal caudals) ; collar well marked ; ventral scales smooth, truncate, strongly overlapping or not, in six to ten longitudinal rows. Toes cylindrical or compressed, usually tubercular beneath (occasionally strongly keeled) ; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern absent in most although not all species. Belly often, but not always, brightly coloured in at least the breeding males.

SPECIES REFERRED. *agilis*, *andreanszkyi*, *armeniaca*, *bedriagae*, *brandtii*, *cappadocica*, *caucasica*, *chlorogaster*, *cyanura*, *dahli*, *danfordi*, *derjugini*, *dugesii*, *fraasii*, *graeca*, *horvathi*, *jayakari*, *laevis*, *lepida*, *monticola*, *mosorensis*, *oxycephala*, *parva*, *perspicillata*, *praticola*, *princeps*, *rostombekovi*, *rudis*, *saxicola*, *schreiberi*, *strigata*, *trilineata*, *unisexualis*, *viridis*, *vivipara*.

Lacerta as defined here is an extremely varied genus within which only one species group can be clearly separated ; this is *Lacerta* part I which is more or less equivalent to *Lacerta* s. str. and will be dealt with separately ; the remainder of the genus forms *Lacerta* part II. I do not propose to use formal subgenera for these two groupings, especially as the type species of *Zootoca* (available for *Lacerta* part II) is rather anomalous.

LACERTA part I (= *Lacerta* s. str.)

Species referred. *agilis, lepida, princeps, schreiberi, strigata, trilineata, viridis.*

Distinguishing features. A closely related group of species distinguished from the rest of *Lacerta* by possession of the following combination of characters. Body-size medium to very large (adults 70 mm to over 210 mm snout to vent) ; skull undepressed, very robust, often with ossified temporal skin. Usually two postnasal scales, dorsals strongly raised, often keeled ; collar strongly serrated, ventrals with very marked imbrication, in six to ten longitudinal rows ; sexual dichromatism in dorsal pattern quite frequent ; in young, dorsum often ocellated or with pale, narrow stripes, dorsal ground colour of adults often bright green, belly white in young, yellowish in adults, never brightly coloured.

Skeletal features. Skull robust ; undepressed with a thick osteodermal layer. Supraocular lamellae complete in non-juvenile specimens, temporal ossification often extensive (not *agilis* or some populations of *trilineata*). Postorbital and postfrontal bones usually separate in hatchlings (not *schreiberi*) but sometimes fused in adults (always in *lepida*) ; pterygoid teeth nearly always present. Sex-correlated variation in the number of presacral vertebrae present ; commonest numbers 27 in males and 28 in females (often 28 and 29 respectively in *agilis*). Clavicle expanded medially, exists in both intact and emarginated conditions in all species. Interclavicle cruciform, lateral arms not obviously directed forwards or backwards. Sternal fontanelle oval, occasionally imperforate. Usually one, two or even three pairs of inscriptional ribs. Typically five or six non-autotomic tail vertebrae (rarely seven, four in some *agilis*). Caudal pattern most frequently B, less often A (some *agilis, schreiberi* and *viridis*).

Hemipenis. Symmetrically bilobed without an obvious armature ; lobes not folded in retracted organ, plicate. Apical sections of lobes subequal to or shorter than basal sections ; lobe tips without prominent papillae. Lips of lobe sulci small to moderate. Micro-ornamentation variable ; *L. lepida* has simple recurved spines but in most species the lobe apices have short tubercles with a fine denticulation at their tips, while the lobe flanks are covered by long, fairly straight projections that sometimes end in a point and sometimes in an irregular series of spinules. In *L. princeps* these flank spines tend to be recurved.

External features. Medium to large lizards (adults from about 70 mm to 210 mm snout to vent). Nostril in contact with first upper labial and usually bordered posteriorly by two postnasals (one in many *agilis*). Eyelid scaly.

Parietal shield not clearly emarginated, but its outer margin generally running medial to the postorbital–postfrontal suture if present. In most cases, two large, deep supratemporals (posterior one sometimes broken into two or three parts). Masseteric shield frequent. Dorsal scales small to moderately large, 32 to 98 across the mid-body, raised and usually strongly keeled (keeling weak or absent in *lepida*). Collar well developed, strongly serrated. Ventrals smooth, truncate, strongly imbricating, in six to ten longitudinal rows, their borders forming laterally inclined parallelograms. Preanal scale large in most cases (somewhat reduced in *L. lepida* and to a lesser extent in *L. schreiberi* and some *L. trilineata*). Toes tubercular beneath, not strongly compressed. Femoral pores usually present, each series extending to knee (except in some *L. trilineata*), 11 to 22 pores in each series. Tail long, unmodified.

Coloration. Sexual dichromatism occurs in a number of populations and is particularly well developed in *L. schreiberi* and many *L. agilis*. In juveniles the dorsum often has up to seven light longitudinal stripes although these may be absent (especially some *lepida*, *trilineata* and *viridis* which are uniform) or replaced by ocelli (many *agilis* ; *lepida* and *schreiberi*). In adults the stripes, if originally present, are frequently lost and the dorsum becomes bright green (not in *princeps*, or some *agilis*, *lepida*, *viridis*, *schreiberi* and *strigata*). Dorsum may sometimes be heavily marked with black (especially some *agilis* and female *schreiberi*) but lizards of this group lack the dark lateral bands often found in *Lacerta* part II, *Podarcis*, *Gallotia*, *Algyroides* and *Psammodromus*. The throat is often brightly coloured in breeding males (not *L. lepida* and some populations of *agilis*, *strigata*, *trilineata* and *viridis*), but this does not apply to the belly which never contrasts strongly with the dorsum and which also always lacks blue spots on the outer ventral scales.

Relationships. The seven species that make up *Lacerta* part I form a tight, closely related assemblage, the members of which have a detailed morphological similarity to each other. However Peters (1961, 1962a) has suggested that *L. princeps* and *L. lepida* have no near relationship to the other species and indeed this author placed *L. lepida* in *Gallotia*. Among the grounds given for excluding *princeps* from *Lacerta* part I are (i) its large dorsal scales, (ii) lack of green pigment and (iii) the presence of ' real ' (i.e. black-bordered) blue lateral ocelli. Eiselt (1968) regards these differences as unimportant and certainly they seem rather trivial compared with the overall resemblance of *princeps* to other *Lacerta* part I lizards. Although the dorsal scales are large they are approached in size by those of some populations of *L. strigata*, a geographical neighbour of *princeps* ; also the differences in scale size within *Lacerta* part I (as defined here) are not particularly large, being considerably less than those found in *Gallotia*. Absence of green dorsal coloration is not confined to *princeps*, it occurs as well in some members of other species (see above). Similarly the presence of black-bordered, lateral ocelli is not really distinctive, indeed they do not occur in all *princeps* being typical only of the nominate subspecies ; *L. p. kurdistanica* Suchov 1936 has simple, unbordered blue spots on the flanks similar to those occurring in some *L. trilineata*. The blue ocelli of adult *L. p. princeps* appear to develop from paler ocelli in juveniles (see photographs in Eiselt 1969) which are very similar to the ocelli found in juveniles of *L. schreiberi.*

The case for transferring *L. lepida* to *Gallotia* must also be rejected. Peters (1961) again cites the presence of blue ocelli as grounds for exclusion from *Lacerta* s. str. (= *Lacerta* part I), but as in *L. princeps*, those of *L. lepida* develop from white ocelli which are also found in juveniles of some other *Lacerta* part I species. Furthermore, some *L. lepida* have no lateral ocelli at all.

Admittedly members of *Gallotia* have bright (blue or yellow) flank spots but these are not clearly dark-edged. Bright flank-markings seem often to be sign stimuli and are likely to develop in any forms that use a lateral display in courtship or in aggressive activities ; on their own therefore they do not necessarily indicate relationship. Other resemblances between *L. lepida* and the large members of *Gallotia* pointed out by Peters are : small anal plate surrounded by many small scutes ; high counts for dorsal scales across mid-body, longitudinal rows of ventrals, gular scales between chin-symphysis and collar, caudal scales in a basal whorl and femoral pores. All these characteristics indicate a general reduction in relative scale-size. It has already been pointed out (p. 313) that this is often correlated with large body-size and dry habitats, conditions that apply both to *L. lepida* and to *Gallotia* so again this resemblance may be convergent. More important *L. lepida* agrees with the majority of species in *Lacerta* part I in a long series of characters not found in *Gallotia*, viz. postorbital and postfrontal bones separate in juveniles, sexual variation in presacral vertebral number (usually 27 in males and 28 in females as against 26 (rarely 25) in both sexes in *Gallotia*), clavicle sometimes emarginate, AB type caudal vertebrae, hemipenis without large apical papillae, two postnasals present, green dorsal colouring and no bright belly pigment. It seems certain therefore that the affinities of *L. lepida* do lie with *Lacerta* part I. Within this grouping, *L. lepida*, particularly the northwest African *L. l. pater*, has a considerable resemblance to *L. trilineata* and especially *L. schreiberi. L. l. pater* is similar to the latter in having eight rows of ventral shields, a small preanal, spotted juvenile livery and early fusion of the postorbital and postfrontal bones (before hatching in *schreiberi*, soon afterwards in *lepida pater*). The head shape and male colouring are also very close.

Contrary to the opinions of Boulenger (1916) *Lacerta* part I is not closely related to *Gallotia* nor does it have any clear relationship with *Podarcis*. Its members are, however, very similar in skeletal and hemipenial features to some species of *Lacerta* part II.

DISTRIBUTION (see Fig. 12). Extensive and continuous, covering much of the total range of the genus *Lacerta* (except some parts inhabited only by *L. vivipara*, some islands etc.). N.W. AFRICA : Morocco, N. Algeria, N.W. Tunisia (perhaps Rio de Oro – Valverde 1957). MAINLAND EUROPE : Southern peninsulas north to England, Denmark, Sweden, south Finland and about latitude 60° in Russia. MEDITERRANEAN ISLANDS : Sicily, Elba, islands on eastern Adriatic coast, Ionian Islands, Corfu, Crete, Cyclades, Euboa, Rhodes, Lesbos and several other Aegean islands. WESTERN ASIA : Central Asia to Turkey, east Mediterranean coast south to Israel, N. Iraq, N. and western Iran south to Shiraz and Neyriz.

Biology. *Lacerta* part I species are usually among the largest lizards occurring in their ranges. They tend to eat larger prey than other sympatric lacertid species and thus avoid competition with them. Most forms are typically associated with areas having dense bushy vegetation (or occasionally with rough grass-land). *L. agilis* is mainly ground-dwelling but the other species may climb in bushes or even trees ; they do not climb on rock surfaces to any great extent.

LACERTA part II

Species referred. *Lacerta* part II contains members of *Lacerta* that do not possess the combination of characters distinguishing *Lacerta* part I.

Distinguishing features. Most species are under 90 mm snout to vent when adult and have brightly coloured bellies in at least the breeding males. *L. jayakari*, however, is much larger (up to 165 mm) and appears to lack a bright belly at all times ; in spite of this its affinities appear to lie with other members of *Lacerta* part II.

Skeletal features. Skull variable, depressed and delicate in some species, very robust in others, many forms intermediate between these two extremes. Supraocular lamellae often fenestrated and external nares rather large in adults of about half the species ; temporal ossification usually absent. Postorbital and postfrontal bones usually unfused (fused in *L. vivipara*) ; pterygoid teeth usually absent (not *L. brandtii*, *L. dugesii*, *L. jayakari* and *L. laevis*). Presacral vertebral number shows sex-correlated variation : usually between 25 and 28 in males, 26 and 29 in females. Clavicle expanded medially and existing in both intact and emarginated conditions in most forms (perhaps only the intact condition present in *L. parva* and *L. fraasii*). Interclavicle cruciform with lateral arms usually not strongly directed forwards or backwards (angled distinctly backwards in *L. dugesii* and *L. perspicillata*). Sternal fontanelle usually oval. (It may approach the cordiform condition in *L. laevis*, *L. andreanszkyi* and *L. danfordi*.) Inscriptional ribs often absent or only one pair present. Non-autotomic caudal vertebrae most usually number 5 or 6, less commonly 4 and rarely 7. Tail vertebrae frequently B pattern or, less often, A : *L. d. danfordi* and *L. d. anatolica* but not *L. d. kulzeri* are peculiar in having C-type vertebrae while *L. brandtii*, *L. fraasii* and *L. parva* have caudal sequences more or less intermediate between the B and C types.

Hemipenis. Symmetrically bilobed ; in most cases no obvious armature and the lobes not folded in repose ; armatures and complexly folded lobes do occur in *L. vivipara*, *L. cyanura* and *L. jayakari* and a more limited armature development may occur in *L. cappadocica* and *L. graeca*. Outer surfaces of lobes usually regularly plicate but not in *L. parva* or *L. fraasii* where the walls of the retracted organ are arranged in irregular folds and have longitudinal flaps. Lobes without large apical papillae ; their sulcal lips usually small or very small (larger in *andreanszkyi*, *danfordi*, *perspicillata* and *laevis*).

Micro-ornamentation variable : most forms have crown-shaped tubercles but simple recurved spines occur in *andreanszkyi*, *bedriagae*, *cappadocica*, *graeca*, *jayakari* and *perspicillata*. *L. dugesii* has spines that at first sight appear simple but when examined with a scanning electron microscope can be seen to have a number of spinules at their tips so that they are intermediate between the two types of ornamentation mentioned so far. *L. brandtii*, *L. fraasii* and *L. parva* all have irregular tubercles that seem to end in spinules. They often appear bifurcate but this is uncertain in the case of *brandtii*. (Micro-ornamentation data from Böhme 1971, and personal observations.)

The above comments on hemipenial structure do not cover the apparently all-female parthenogenetic forms allied to *L. saxicola*, viz. *armeniaca*, *dahli*, *rostombekovi* and *unisexualis*.

External features. Small to large lacertids: adults from about 35 mm (*andreanszkyi*) to 165 mm (*jayakari*) snout to vent, but most species between 50 mm and 90 mm. Nostril usually in contact with first upper labial (often narrowly separated in some species, e.g. *andreanszkyi, brandtii, cappadocica, fraasii, monticola, parva, perspicillata, vivipara*), bordered posteriorly by one or two superposed postnasals (three in some *L. cappadocica*), usually one in about half the species, one or two in *bedriagae, fraasii* and *mosorensis*, two in the remainder, viz. *brandtii, cappadocica, cyanura, danfordi, dugesii, graeca, jayakari, laevis, oxycephala, parva* and *perspicillata*. Eyelid fairly opaque and scaly in most forms; a window of transparent, black-edged scales in *L. cappadocica*, a single-scaled window in *L. perspicillata*. Anterior part of lateral border of the parietal shield often emarginated and running medial to the edge of the postorbital bone in the majority of species but along the postorbital margin in *andreanszkyi, dugesii, perspicillata, vivipara* and some *bedriagae*. Supratemporals well developed in most cases, the first usually being longer and deeper than the rest; sometimes the supratemporals not easily distinguishable from temporals, e.g. particularly *dugesii, perspicillata*. In *cappadocica, cyanura* and *jayakari* all the supratemporals rest at least partly on the bony parietal table; in *jayakari* the posterior supratemporals are diagonally enlarged so that the anterior of each lies above the posterior portion of the one in front. Masseteric shield usually distinguishable in most species but not in *cappadocica, cyanura, dugesii, graeca, jayakari, perspicillata* and many *andreanszkyi, bedriagae, danfordi* and *oxycephala*. Dorsals small, 25 (some *vivipara*) to 91 (some *jayakari*) in a transverse series at mid-body, in most species smooth or faintly keeled but more strongly so in *chlorogaster, laevis, parva, praticola, rudis* and *vivipara*. Collar well developed, serrated or smooth. Ventrals smooth, truncate, the degree of imbrication varying with habitat (least in rock-dwellers, greatest in ground forms); usually in six longitudinal rows (exceptions: *brandtii* eight to ten, *jayakari* and *parva* eight, *perspicillata* ten; some individuals of *cappadocica, danfordi, fraasii* and *laevis* may also have eight rows). Preanal shield usually large, occasionally rather reduced with two or more semicircles of small scales anterior to it, e.g. *cappadocica, danfordi, fraasii, jayakari, parva*. Toes varying in degree of compression, usually tubercular beneath but unicarinate in *L. cappadocica*, strongly bicarinate in *L. cyanura* and weakly so in some *L. parva*. Femoral pores present, extending to, or nearly to knee; 7 (some *vivipara*) to 31 (some *bedriagae*) in each series. Tail long, unmodified.

COLORATION. Sexual dimorphism in dorsal patterning of adults absent in most forms (few exceptions, e.g. *L. dugesii* and to a lesser extent some populations of *L. monticola* and in *L. graeca*). Pattern very variable but most species lack the lateral pairs of *narrow*, well-defined pale stripes found in *Podarcis* and *Gallotia* (they are often present in *andreanszkyi*, *parva* and *vivipara*). Pattern usually consists of dark longitudinal stripes or series of markings which sometimes coalesce to form a reticulation (e.g. *bedriagae*, *jayakari*, *oxycephala*). In *cappadocica*, *danfordi* and *perspicillata* there seem to be distinct colour-morphs, the last two species including individuals with almost no markings, perhaps equivalent to the ' concolor ' morph of *Podarcis*. Venter usually brightly pigmented, particularly in breeding males although both sexes are often involved. *L. jayakari* appears to be exceptional in lacking any bright ventral coloration. The outer ventrals often have blue spots and these may extend onto the flanks in some cases.

RELATIONSHIPS. *Lacerta* part II unlike the other groupings discussed in this paper contains a very varied assemblage of species (many of their principal differences are summarized in Table III). It includes all the species originally assigned to the subgenera *Zootoca*, *Archaeolacerta*, *Apathya* and *Scelarcis* plus many of the species of uncertain position listed on pp. 298–299 and *Lacerta dugesii* which is usually classified with *Podarcis* (group 3). Many of the characters on which these subgeneric divisions were based appear to be ecologically labile and are thus relatively unimportant in assessing relationships (see pp. 315–324) ; once they are excluded from consideration, *Lacerta* part II in spite of its variability cannot be divided into discrete groups although it is often possible to suggest which forms are particularly closely related. However, for convenience, *Lacerta* part II will be discussed under a number of separate headings, even although the divisions between them are to a large extent artificial.

(a) The more typical members of *Lacerta* part II.

SPECIES DISCUSSED. *armeniaca*, *bedriagae*, *caucasica*, *chlorogaster*, *dahli*, *danfordi*, *derjugini*, *graeca*, *horvathi*, *laevis*, *monticola*, *mosorensis*, *oxycephala*, *praticola*, *rostombekovi*, *rudis*, *saxicola*, *unisexualis*.

The above species occur in a broad, but disjunct band from northern Spain and Portugal across the northern Mediterranean region to the Caucasus and south Caspian coastal area. The majority of these forms have all the features listed as characteristic of *Lacerta* part II (although this does not necessarily imply that they are primitive). This applies especially to the more northern ones ; some of the southern species are rather different, frequently having two postnasals (*danfordi*, *graeca*, *laevis*, *oxycephala* and some *bedriagae* and *mosorensis*) and the masseteric shield absent or often reduced (*bedriagae*, *danfordi*, *graeca* and *oxycephala*). These southern species are often better differentiated than the more northern ones and some possess peculiar features. For instance, some populations of *L. danfordi* have C-type caudal vertebrae and very large sulcal lips on the hemipenis ; *L. laevis* and some *L. danfordi* often have a more or less cordiform sternal fontanelle and *L. graeca* has a distinct armature development in the hemipenis and simple spines (as opposed to tubercles with a ring of spinules at their tips) on the hemipenial

T e easily appreciated.
I presently available.

	chlorogaster	*praticola*	*derjugini*	*caucasica*	*rudis*	*saxicola*-group	*vivipara*
Clear armature present	–	–	–	–	–	–	+
Postorbital and postfrontal bones	–	–	–	–	–	–	+
No microchromosomes in karyoty	–	–	–	–	–	–	+
Parietal shield extends to outer ec postorbital bone	–	–	–	–	–	–	+
Lateral arms of interclavicle clear posteriorly	–	–	–	–	–	–	–
Masseteric shield absent or reduce	–	–	–	–	–	–	–
Two postnasal scales present	–	–	–	–	–	–	–
Hemipenial micro-ornamentation spines (+) or irregular often bifur tubercles (×)	–	–	–	–	–	–	–
Eight or more rows of ventral sca	–	–	–	–	–	–	–
Prominent blue spots on flanks	+	–	–	–	–	(+)	–
Caudal vertebrae not of A or B ty	–	–	–	–	–	–	–
Hemipenial lobes with longitudina unplicate	–	–	–	–	–	–	–
Chromosome number greatly redu	–	–	–	–	–	–	–
Sternal fontanelle approaches hea	–	–	–	–	–	–	–
Very large body-size	–	–	–	–	–	–	–
Supratemporal scales diagonally e	–	–	–	–	–	–	–
Supratemporal scales all rest on sl	–	–	–	–	–	–	–
Belly always pale, without bright even in breeding males	–	–	–	–	–	–	–
Toes carinate beneath	–	–	–	–	–	–	–
Lower eyelid with 'window'	–	–	–	–	–	–	–
Strongly expanded scales under fo	–	–	–	–	–	–	–

TABLE III: Distribution of characters present in a minority of *Lacerta* Part II species

The characters are arranged not according to anatomical proximity but so that the common features of each loose species-group can be easily appreciated. Parentheses indicate that the character is only sometimes present or present in limited form, a question-mark that no certain data are presently available.

	fraasi	*parva*	*brandtii*	*andreanszkyi*	*perspicillata*	*dugesi*	*jayakari*	*cyanura*	*cappadocica*	*laevis*	*danfordi*	*graeca*	*bedriagae*	*oxycephala*	*monticola*	*mosorensis*	*horvathi*	*chlorogaster*	*praticola*	*derjugini*	*caucasica*	*rudis*	*saxicola-group*	*vivipara*
Clear armature present	–	–	–	–	–	–	+	+	(+)	–	–	(+)	–	–	–	–	–	–	–	–	–	–	–	+
Postorbital and postfrontal bones fused	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+
No microchromosomes in karyotype	?	+	?	?	?	?	?	?	?	–	?	?	?	–	?	?	?	–	–	–	–	–	–	+
Parietal shield extends to outer edge of postorbital bone	–	–	–	+	+	+	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–	+
Lateral arms of interclavicle clearly directed posteriorly	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Masseteric shield absent or reduced	–	–	–	(+)	+	+	+	+	+	–	(+)	+	(+)	(+)	–	–	–	–	–	–	–	–	–	–
Two postnasal scales present	(+)	+	+	–	+	+	+	+	+	+	+	+	(+)	+	–	(+)	–	–	–	–	–	–	–	–
Hemipenial micro-ornamentation of simple spines (+) or irregular often bifurcate tubercles (×)	×	×	× ?	+	+	(+)	+	–	+	–	–	+	+	–	–	–	–		–	–	–	–	–	–
Eight or more rows of ventral scales	(8)	8	8/10	–	10	–	8	–	(8)	–	(8)	–	–	–	–	–	–		–	–	–	–	–	–
Prominent blue spots on flanks	+	+	+	–	–	–	–	–	–	–	+	(+)	–	–	–	–	–	+	–	–	–	–	(+)	–
Caudal vertebrae not of A or B type	+	+	+	–	–	–	–	–	–	–	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–
Hemipenial lobes with longitudinal flaps; unplicate	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	–	–	–
Chromosome number greatly reduced	?	+	?	?	?	?	?	?	?	–	?	?	?	–	?	?	?		–	–	–	–	–	–
Sternal fontanelle approaches heart-shape	–	–	–	(+)	–	–	–	–	–	+	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–
Very large body-size	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Supratemporal scales diagonally enlarged	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Supratemporal scales all rest on skull table	–	–	–	–	–	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Belly always pale, without bright colour, even in breeding males	–	–	–	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Toes carinate beneath	–	(+)	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–		–	–	–	–	–	–
Lower eyelid with 'window'	–	–	–	–	+	–	–	–	+	–	–	–	–	–	–	–	–		–	–	–	–	–	–
Strongly expanded scales under forearm	–	–	–	–	–	–	+	+	(+)	–	(+)	–	–	–	–	–	–	–	–	–	–	–	–	–

epithelium; similar spines occur in *L. bedriagae* (Böhme 1971). Many of the northern species, on the other hand, are very similar to each other, indeed some of the key characters allegedly distinguishing allopatric forms do not always do this. This is true for *L. horvathii* and *L. mosorensis*. It seems probable that the geographical isolation of some of these northern species may be a relatively recent occurrence.

(b) *Lacerta vivipara.*

This species has an immense and largely continuous distribution mainly to the north of the area occupied by the species discussed in the last paragraph. It is probably related to the more northern of these forms but it differs from them all in a number of features: the hemipenis has a well-differentiated armature and folded lobes, the postorbital and postfrontal bones are fused even in newly deposited young, the edge of the parietal shield reaches the outer margin of the bony parietal table, one pair of microchromosomes is lacking from the usual *Lacerta* karyotype (which is present in the 12 typical members of *Lacerta* part II that have been investigated to date; see p. 310) and unlike the rest of *Lacerta*, *L. vivipara* is ovoviviparous over most of its range.

L. vivipara is usually associated with *L. derjugini* and *L. praticola* in the subgenus *Zootoca* but there are no good grounds for doing this. The resemblance between the three species (body-shape, rather large dorsal scales, serrated collar, some overlapping of ventrals, often complete supraocular lamellae) is connected with their similar habitats – all are ground-dwelling lizards occurring most usually in rather moist herbaceous places (Lantz & Cyrén 1947). Neither *L. derjugini* nor *L. praticola* has any of the *vivipara* characters listed above, instead they are very similar to the other typical members of *Lacerta* part II in their general features and it is almost certain that this is where their close affinities lie, indeed *L. derjugini* frequently hybridizes in the wild with one of the typical species, *L. saxicola* (Darevsky 1966).

(c) Southeastern species.

SPECIES DISCUSSED. *cappadocica, cyanura, jayakari.*

These three well-defined species have some resemblance to each other. Like the more southern typical members of *Lacerta* part II they have two post-nasal scales (three in some *L. cappadocica*) and no masseteric shield. In addition all their supratemporals rest on the parietal table and they have at least some indication of an enlarged series of scales beneath the forearm. *L. cappadocica* and *L. jayakari* both have the hemipenial epithelium micro-ornamented with simple recurved spines while that of *L. cyanura* has crown-shaped tubercles.

L. cappadocica has a number of rather peculiar features: its hemipenis may have a fairly weak but definite armature and the lobes of the hemipenis may be somewhat folded, the parietal shield has a concave lateral margin, the eyelid a transparent window of black-edged scales and the digits a single row of keels beneath. Although quite distinct from it, this species probably has affinities with its geographical neighbour, *L. danfordi*, which it resembles in some features of head-scaling, in body proportions in similar polymorphic colour patterns and in their both often having a series of feebly enlarged scales beneath the forearm.

L. jayakari resembles *L. cappadocica* in the features common to the three south-eastern species and also in possessing a hemipenial armature and folded hemipenial lobes. However, the armature and lobe-folding are much better developed than in *L. cappadocica* and the degree of enlargement in the scales under the forearm is much greater. *L. jayakari* also differs from *L. cappadocica* and from the greater part of *Lacerta* part II in its large size, lack of belly pigment (apparently even in breeding males), diagonally elongated posterior supratemporals and its strongly keeled, straight caudal scales. In the first two characters it resembles *Lacerta* part I but does not possess the other features characteristic of the members of that group.

L. cyanura, which is sympatric with *L. jayakari* in Oman, seems to have close affinities with this species in spite of its much smaller size and possession of bright belly colouring (blue) in the male (Arnold 1972). The two species are alike in most skeletal features including the number of presacral vertebrae in females (26), most aspects of hemipenial structure, the very enlarged plates under the forearm and the strongly keeled caudal scales. The pattern of the one known juvenile has some resemblance to that found in the *wolteri* Bird 1936 form of *L. cappadocica*. Sub-digital keeling is also found in both *L. cyanura* and *L. cappadocica* but the pattern differs, *L. cyanura* having two rows of keels beneath each digit and *L. cappadocica* one.

In spite of their considerable differences it is likely that the two Oman species are closer to *L. cappadocica* than to any other member of *Lacerta*.

(d) Southwestern species.

SPECIES DISCUSSED. *andreanszkyi, dugesii, perspicillata.*

One of these species, *L. dugesii*, has usually been classified with the members of *Podarcis* but it lacks many of the features that occur in all members of that genus and to be much closer to members of *Lacerta* part II especially the other southwestern species. Among the features it possesses that do not occur in *Podarcis* are the following. (1) Interclavicle with lateral arms directed posteriorly. (2) Oval sternal fontanelle. (3) A and B pattern caudal vertebrae. (4) Hemipenis with short apical sections to the lobes and small sulcal lips. (5) Almost always two superposed postnasals. (6) No masseteric shields or well-defined supratemporals. (7) Often a dorsal pattern including rather broad pale supraciliary stripes that become broader and fainter posteriorly (similar to that found in some members of *Lacerta* part II, e.g. *L. caucasica*) ; other specimens have a reticulated or striated pattern rather like that of some *L. perspicillata*. (8) Hemipenial ornamentation consisting of recurved spines with minute spinules on their tips.

The three southwestern species are alike in having the parietal shield reaching the edge of the postorbital bone, in usually lacking the masseteric shield (a masseteric sometimes present in *andreanszkyi*) and in having a micro-ornamentation of more or less simple spines on the hemipenial plicae (distinctive pattern of *L. dugesii* is mentioned above). Each species is well differentiated from the others and has its own peculiarities but, as with the southeastern species, each pair of the trio has features in common that, with the characters listed above, suggest that they are perhaps quite nearly related. Thus *L. perspicillata* and *L. dugesii* both have a peculiar interclavicle structure, two postnasals and similarity in dorsal patterns ; *L. andreanszkyi* and *L. dugesii* have six rows of ventrals and *L. andreanszkyi* and *L. perspicillata* share very large sulcal lips on the hemipenial lobes. *L. perspicillata* has customarily been separated from the rest of *Lacerta* in the subgenus *Scelarcis* because it has ten longitudinal rows of ventrals and a brille in the lower eyelid. Ten rows of ventrals occur elsewhere in *Lacerta* part II (in some *L. brandtii*) and, as explained on p. 311, windows in the lower eyelid are a relatively frequent development in several lines of lacertids ; indeed *L. dugesii* has a number of enlarged and translucent scales in this region. Therefore it does not seem necessary to separate *L. perspicillata* from the rest of *Lacerta* part II on these grounds.

It is uncertain how the three southwestern species relate to the rest of *Lacerta* part II. Their nearest geographical neighbour is *L. monticola* of the northern and central Iberian Peninsula but this species, which appears to have its closest affinities with the more typical members of *Lacerta* part II (see p. 336), does not resemble the southwestern species very closely. The latter have more in common with *L. danfordi* and neighbouring species in the eastern Mediterranean region. Like them they may have two postnasals, no masseteric shields and large hemipenial lips. There is also some resemblance in habitus and in dorsal patterns, especially those of *L. danfordi* to *L. dugesii* and *L. perspicillata*. Such a relationship would not be entirely unexpected as there are other cases of zoogeographical links between the eastern Mediterranean region and Northwest Africa. (The nearest relations of the following Northwest African species, *Acanthodactylus erythrurus* (Schinz) and *A. savignyi* (Audouin), *Ophisaurus koellikeri* (Günther) and *Vipera lebetina mauritanica* (Gray) seem to be respectively *Acanthodactylus tristrami* (Günther), *Ophisaurus apus* (Pallas) and *Vipera l. lebetina* (Linnaeus) which are all essentially east Mediterranean forms. The southwestern species may also have some affinities with *Podarcis*, see p. 355.)

(e) *Lacerta parva* and its relations.

SPECIES DISCUSSED. *brandtii, fraasii, parva.*

As Peters (1962) has pointed out, two of these species, namely *L. parva* and *L. fraasii*, have a considerable external resemblance to each other and this author thought that they were closely related but set somewhat apart from the rest of *Lacerta*. The close affinity of the two species is confirmed by their internal morphology. Both species have similar skeletons with most commonly 28 presacral vertebrae in males and 29 in females, unemarginated clavicles in all the specimens examined and tail vertebrae that are peculiar in being intermediate between the B and C patterns. In both, the hemipenes are unlike those of any other *Lacerta* in lacking regular plicae and having longitudinal flaps on the lobes instead. The hemipenial micro-ornamentation consists of irregular, sometimes bifurcate tubercles. *L. parva* is also singular in having a very reduced chromosomal formula ($2n = 24$)

(Gorman 1969) and is the only species of the genus known to have this degree of reduction. The karyotype of *L. fraasii* has not been investigated to date.

L. parva and *L. fraasii* would occupy an isolated place in the genus if it were not for *L. brandtii* which is morphologically intermediate between these forms and the more typical members of *Lacerta* part II. *L. brandtii* shares the following characters with *L. parva* and *L. fraasii* : tail vertebrae intermediate between the B and C patterns, two postnasals present, nostril often narrowly separated from the first upper labial, often eight longitudinal rows of ventrals, usually two well-separated series of dark markings on the perivertebral area, well-marked blue ocelli on the flanks and perhaps similar hemipenial micro-ornamentation. It differs from them in having a lower presacral vertebral count (26 in males, 27 in females), usually emarginated clavicles, and a hemipenis with clearly defined plicae on the lobes and no longitudinal flaps. In all these features it agrees with at least some of the less aberrant members of *Lacerta* part II.

DISTRIBUTION (see Figs. 12 and 13). Members of *Lacerta* part II are scattered over almost the whole range of *Lacerta*, but with the exception of *L. vivipara*, which is found over an enormous area, the species have small or disjunct ranges. This is almost certainly a relict distribution and indicates that the group has undergone considerable reduction in the area of its total range. In the more southern regions many of the allopatric species are strongly differentiated, probably indicating that their separation is of long standing but, in the north, the species are more similar to each other and here the reduction in range presumably was rather more recent. It is uncertain what caused the shrinkage in distribution ; most species are now confined to relatively moist or highland habitats (exceptions : some *L. danfordi* – Mediterranean islands ; *L. dugesii* – oceanic islands ; *L. brandtii*, *L. fraasii* and *L. parva* – steppe-type habitats) ; possibly the post-glacial temperature-increase may be important. It is difficult to assess how relevant the spread of *Podarcis* has been in this process ; these lizards seem to be better adapted to drier and warmer environments than the members of *Lacerta* part II. Where the two groups occur together, the latter seems best able to compete at high altitudes and, where the two groups are found living side by side, the *Lacerta* part II species usually occupy scansorial or moist terrestrial niches. Whether there has been active elimination of *Lacerta* part II populations by direct competition is uncertain. Certainly the expansion of *Podarcis* can only have been one of several factors in the reduction of the range of *Lacerta* part II, as the latter has undergone an apparent contraction in distribution in many areas where *Podarcis* does not occur.

BIOLOGY. The members of *Lacerta* part II are mainly small lizards that occupy a wide variety of structural niches but the great majority are adapted to living on and around rock faces, the principal exceptions being as follows. *L. chlorogaster* spends considerable amounts of time on tree-boles (Lantz & Cyrén 1947, Terentiev & Chernov 1965, Droedov 1967) and this may originally have been the main habitat of *L. laevis* (e.g. Böhme 1971, Zinner 1967). This would ' explain ' why these species lack certain of the characters of their close relatives originally placed in the subgenus *Archaeolacerta*, viz. smooth, flattened dorsal scales and strongly depressed skull with incomplete ossification of the supraocular lamellae, these features being adaptations to utilizing rock crevices as hiding-places (see p. 320). *L. brandtii*, *L. fraasii* and *L. parva* all occur on the ground in relatively dry and open habitats (Lantz & Cyrén 1939, Wettstein 1928). *L. derjugini*, *L. praticola* and *L. vivipara* also tend to be ground-dwelling but in damp places (Lantz & Cyrén 1947). *L. andreanszkyi* does not climb high on rock faces but is at least partly saxicolous, often occurring on stones and coarse gravel in or near streambeds (K. Klemmer, personal communication ; S. D. Busack, personal communication). *L. dugesii* is often scansorial but occupies a wide range of habitats. There is some evidence that at least the more northern species may operate at rather lower preferred temperatures than sympatric species of *Podarcis* (personal observations on *L. horvathi*, *L. mosorensis*, *L. oxycephala*, *L. monticola* and *L. vivipara* and on *P. melisellensis*, *P. muralis* and *P. sicula*).

ALGYROIDES Bibron & Bory

Bibron & Bory, 1833, *in* Bory, *Expéd. sci. Morée*, **3**, 1 : 67.

Type species. *Algyroides moreoticus* Bibron & Bory.

Diagnosis. Small lacertids (adults not usually over 70 mm snout to vent). Skull fairly robust or delicate and depressed, parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones unfused ; clavicle strongly expanded medially and exists in both emarginated and unemarginated conditions in all species ; interclavicle cruciform, the lateral arms not strongly directed forwards or backwards ; sternal fontanelle usually oval ; sexual variation in presacral vertebral count present ; all presacral vertebrae, except the first three cervicals, with ribs ; free ribs divided into two series, an anterior one of long ribs and a posterior series of short ones ; caudal vertebrae of the A or B pattern.

Hemipenis symmetrically bilobed with no obvious armature, the lobes unfolded in repose and regularly plicate with variable micro-ornamentation ; apical region of lobes short with very small sulcal lips ; no large conical papillae at lobe tips.

Head shields normal, nostril usually in contact with first labial scute, normally two superposed postnasal shields (occasionally one) ; lower eyelid scaly ; anteriorly the parietal scute does not extend to the outer margin of the postorbital bone ; first supratemporal shield large ; masseteric shield frequently present.

Dorsal body-scales large (larger than caudals in at least the mid-dorsal region), collar present and well defined ; ventral scales smooth, truncate, not overlapping very strongly, in six longitudinal rows. Toes cylindrical or compressed, tubercular beneath, femoral pores present. Tail unmodified. Sexual dimorphism absent in most species. Belly brightly coloured in breeding males.

Species referred. *fitzingeri*, *marchi*, *moreoticus*, *nigropunctatus*.

Skeletal features. Skull robust in *A. moreoticus* and *A. nigropunctatus*, more delicate and depressed in *A. fitzingeri* and *A. marchi* which also have the osteodermal layer reduced and fenestrated supraocular lamellae. No ossification in the temporal area. Postorbital and postfrontal bones always separate, pterygoid teeth present in *A. moreoticus* and *A. nigropunctatus*. Presacral vertebrae usually 25–26 in males, 26–27 in females (total range 24–28). Clavicle exists in both intact and emarginate conditions in all species. Interclavicle cruciform, the lateral arms not strongly directed forwards or backwards. Sternal fontanelle oval (may approach cordiform condition in some *A. moreoticus*). Inscriptional ribs usually nil, occasionally one pair present. Non-autotomic caudal vertebrae four or five. Caudal pattern usually B, occasionally A.

HEMIPENIS. As diagnosis. Micro-ornamentation consists of recurved spines in *A. moreoticus* and *A. nigropunctatus* and crown-shaped tubercles in *A. fitzingeri*.

EXTERNAL FEATURES. Small lizards (adults from 30 to 70 mm snout to vent). Nostril in contact with first upper labial; normally two postnasals present (exceptions rather frequent in *A. moreoticus*, rare in the other species). Eyelid scaly. Parietal border emarginated running medial to the outer margin of the postorbital bone (this condition least developed in *A. marchi*). Supratemporals well developed, the first larger and deeper than the rest. Masseteric shield usually well defined. Dorsal scales large (larger than the caudals), imbricate, strongly keeled (less so in *A. marchi*), either pointed (*A. fitzingeri*, *A. moreoticus*) or truncate (*A. marchi*, *A. nigropunctatus*); number of dorsals in a transverse series at mid-body 15 to 28. Collar well developed, fairly smooth or serrated. Ventrals truncate, smooth, without very strong overlap, in six longitudinal rows. Preanal shield large, bordered by one or (more rarely) two semicircles of small plates. Toes cylindrical or compressed, tubercular beneath. Femoral pores present, each series extending to the knee and containing 11 to 18 pores. Tail unmodified.

COLORATION. Sexual dimorphism in dorsal pattern absent except in *A. moreoticus*. Most individuals basically brown or bronze-brown above, the flanks often darker (*marchi*, *nigropunctatus*, some *fitzingeri* and male *moreoticus*; the latter also having light spotting on the flanks). Dorsum may have irregular dark spots (*nigropunctatus*, male *moreoticus*), or a vertebral stripe (*marchi*, *fitzingeri*), or be uniform (some *fitzingeri* and *nigropunctatus*, female *moreoticus*). Male *moreoticus* have light, narrow, dorsolateral stripes. Venter brightly coloured in males, the colour extending onto the flanks in *A. nigropunctatus*. Throat and belly may contrast (blue : orange in *nigropunctatus*, blue or white : yellow in *marchi*); blue spots may be present on the outer ventrals.

RELATIONSHIPS. The four species of *Algyroides* are generally quite similar and they seem to constitute a natural group. They resemble each other quite closely in external morphology, osteology, and in having very small sulcal lips on the hemipenial lobes. Externally *A. nigropunctatus* seems most similar to *A. marchi* and *A. fitzingeri* to *A. moreoticus*. The first two species have small lateral scales and truncate dorsals while the last two have no differentiation between dorsals and laterals, all scales being both large and pointed. It is uncertain that these superficial resemblances indicate true relationships; the pattern of hemipenial micro-ornamentation does not support such an arrangement since *A. moreoticus* has simple recurved spines on the lobe plicae which are like those of its geographical neighbour *A. nigropunctatus* and unlike the crown-shaped tubercles occurring in *A. fitzingeri* (the pattern of micro-ornamentation in *A. marchi* is not yet known).

DISTRIBUTION (see Fig. 15). The four species each have relatively small ranges in southern Europe and are completely or almost allopatric (*moreoticus* and *nigropunctatus* coexist in the Ionian Islands). *Algyroides* occurs in southeastern Spain (perhaps also central Spain, see, e.g., Buchholz 1965), Corsica, Sardinia, the eastern Adriatic seaboard as far south as Epirus, the Ionian Islands and southern Greece.

BIOLOGY. There is some evidence that these small lizards were perhaps originally largely associated with semi-shaded woodland habitats (*marchi* – Klemmer 1960, personal observation; *moreoticus* – Clarke 1970, personal observation; *nigropunctatus* – personal observation). Populations are now found in deforested areas but some *Algyroides* occur quite frequently in and around fallen timber and others live among and climb in bushes.

PODARCIS Wagler

Wagler, 1830, *Syst Amph.* p. 154.

TYPE SPECIES. *Seps muralis* Laurenti.

DIAGNOSIS. Small, occasionally medium-sized lacertids (adults not usually over 90 mm snout to vent). Skull usually fairly robust but may be relatively depressed with a fairly thin osteodermal layer; parietal foramen present, frontal bones paired throughout life, postorbital and postfrontal bones unfused; clavicle strongly expanded medially, existing in both emarginated and unemarginated conditions (often within the same population); interclavicle cruciform, the lateral arms not strongly directed forwards or backwards; sternal fontanelle usually heart-shaped; sexual variation in presacral vertebral count present; all presacral vertebrae, except the first three cervicals, with ribs; free ribs in two series, long anterior ones differentiated abruptly from short posterior ones; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature, the lobes unfolded in repose and regularly plicate with a micro-ornamentation consisting of simple, often recurved spines; apical regions of the lobes relatively long (usually longer than basal portions of the lobes) with extremely large sulcal lips; no large conical papillae at lobe tips.

Head shields normal, nostril usually in contact with first upper labial scute and usually bordered posteriorly by a single postnasal shield (occasionally two), eyelid scaly; anteriorly the outer edge of the parietal shield runs along the lateral margin of the postorbital bone; supratemporals present, rather narrow; a masseteric shield frequently present.

Dorsal scales small (less than half the length of the proximal caudals); collar well developed; ventral plates smooth, truncate, not strongly overlapping, in six (rarely eight) longitudinal rows. Toes somewhat compressed, tubercular beneath; femoral pores present. Tail unmodified. Sexual dimorphism in dorsal pattern usual in most populations. Belly usually brightly coloured, at least in breeding males.

SPECIES REFERRED. *erhardii, filfolensis, hispanica,** *lilfordi, melisellensis, milensis, muralis, peloponnesiaca, pityusensis, sicula, taurica, tiliguerta, wagleriana.*

SKELETAL FEATURES. Skull usually fairly robust, sometimes quite depressed with a reduced osteodermal layer, particularly in *P. hispanica*. Supraocular lamellae complete in most adults (some exceptions especially in *P. hispanica*), temporal region usually unossified (fairly extensive ossification in some *P. peloponnesiaca* and traces in individuals of some other forms, e.g. *P. taurica* and *P. melisellensis*). Postorbital and postfrontal bones always separate in hatchlings, occasionally fused in adult males, pterygoid teeth present in at least some individuals of most species (not *P. lilfordi* or *P. wagleriana* fide Klemmer 1957). Presacral vertebral number shows some correlation with sex, 27 commonest number for males (26 in *P. tiliguerta, P. filfolensis, P. muralis* and *P. pityusensis*), 28 in females (27 in *P. filfolensis, P. lilfordi, P. pityusensis* and *P. tiliguerta*) ; males occasionally have 25 presacral vertebrae, females 29. Clavicle expanded medially, most frequently emarginated but some specimens of the majority of species have the bone intact (not in *L. filfolensis* and *L. muralis*). Interclavicle cruciform, the laterally directed arms not strongly angled forward but may occasionally be angled very slightly backwards, especially in *L. wagleriana*. Sternum of most individuals with a cordiform fontanelle having a very distinct, posteriorly directed process arising from its anterior border. One inscriptional rib-pair may be present. Non-autotomic caudal vertebrae usually five or six, sometimes four. Caudal pattern always of the C type.

HEMIPENIS. Symmetrically bilobed without an obvious armature ; lobes not folded in the retracted organ, plicate. Apical sections of the lobes usually longer than basal parts, sometimes subequal ; lobe tips without prominent papillae. Lips on lobe sulci very large, the outer one varying in its mode of attachment to the lobe wall as follows.

P. hispanica, P. muralis : the outer lip is free laterally for its whole length and can be easily reflected to expose its underside which shows traces of the plication that covers the rest of the lobe wall.

All other species : here there is an obvious longitudinal fold in the lobe wall directly dorsal (in the retracted organ) to the lip which is fused to the fold apically but is free basally.

Hemipenial micro-ornamentation in *Podarcis* consists of simple recurved spines (Böhme 1971 ; personal observations).

EXTERNAL FEATURES. Small to medium-sized lizards (adults usually from 50 mm to 80 mm snout to vent, occasionally over 90 mm). Nostril in contact with first upper labial, bordered posteriorly usually by a single postnasal (occasional exceptions, especially unilateral ones). Eyelid scaly. Anteriorly the lateral border of the parietal is unemarginated, usually following or close to the outer edge of the postorbital bone. Supratemporals often distinguishable, rather narrow, the first often the longest ; in some forms supratemporals are small and scarcely separable from the similarly sized temporals (e.g. *hispanica, lilfordi, pityusensis* and some *tiliguerta*). Masseteric present in most individuals but frequently small or absent in *P. hispanica*. Dorsals small, 42 to 90 in a transverse row across the mid-body, usually granular with a raised transverse section (fairly flat in some *P. hispanica*), sometimes smooth or faintly keeled (*erhardii, filfolensis, hispanica, lilfordi, milensis* and *pityusensis*), sometimes quite strongly keeled (*melisellensis, sicula, taurica* and *wagleriana*). Collar well developed, usually fairly smooth-edged but sometimes distinctly serrated (*P. taurica*). Ventrals smooth, truncate, degree of overlap variable but never very strong, arranged in six (rarely eight) longitudinal rows. Preanal shield with one or, more rarely, two semicircles of small scales anterior to it. Toes vary in degree of compression, tubercular beneath. Femoral pores extend to knee, 13 to 29 in each series. Tail long, unmodified.

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* *P. hispanica*, as presently understood, may not be a single species (Klemmer, personal communication).

COLORATION. Sexual dimorphism in the dorsal pattern is usual in adults. Some specimens have continuous longitudinal stripes on the body : there may be a pair of light stripes on each flank (starting from the supraciliary and supralabial regions) ; these may be separated and bordered by dark pigment and there is often a dark vertebral stripe as well. The pattern may vary, for instance particular elements may be absent or divided. In other specimens, the dark stripes are broken up into discrete, although often very irregular transverse bars which in extreme cases may coalesce to form a reticulation. In most forms, the females tend towards the striped condition while the males, by comparison, have the pattern more broken up. This does not apply to certain populations where both sexes have reticulated markings (e.g. *P. f. filfolensis, P. muralis insulanica* and *P. m. nigriventris*). Ground colour is very variable and may be brown, grey or green. In some species there may be a distinct polymorphism in dorsal pattern, some specimens having the normal dark markings while others lack them completely (usually referred to as ' concolor-mutants '). This morph occurs in *P. erhardii, P. filfolensis, P. hispanica, P. melisellensis, P. sicula, P. taurica* and *P. wagleriana*. Insular melanic populations are frequent. Ventral surface usually brightly coloured in breeding males, but not in most mainland populations of *P. sicula*, some populations of *P. peloponnesiaca* (fide Buchholz 1960) or in many *P. milensis* ; other individuals of this last species have only the second rows of ventrals from the midline brightly coloured. Throat and belly may contrast ; the outer ventrals often bear blue spots.

RELATIONSHIPS. The thirteen species of *Podarcis* form a very homogeneous assemblage. *Lacerta dugesii* which used to be classified with these forms in the subgenus *Podarcis* in fact differs from them in many features and is more fully discussed on p. 338. Klemmer (1957) considered *Podarcis peloponnesiaca* to be *incertae sedis* because he felt that its often very robust skull and usually quite extensively ossified temporal region separated it from the other species here placed in *Podarcis*. However, *P. peloponnesiaca* possesses all the features which in combination distinguish *Podarcis* from other lacertid genera (see Diagnosis). The characters that Klemmer thought separate this species from *Podarcis* involve only relatively slight changes in degree of ossification : thus the heavy skull of *P. peloponnesiaca* is approached by that of other *Podarcis* species such as *P. taurica*, especially its southern populations, and other members of this genus may also have some (admittedly minor) temporal ossification, e.g. individuals of *P. melisellensis* and *P. taurica*.

Because the species of *Podarcis* are all morphologically very similar, it is difficult to decide which forms are most closely related to each other. Most attempts to subdivide the group (e.g. Kopfstein and Wettstein 1921, Boulenger 1920, Klemmer 1957) have been based on external morphology, especially skull and body shape and colour pattern. Unfortunately the morphological variables are largely the sort of characters that often correlate fairly closely with the kind of niche occupied and on their own are uncertain indicators of relationship. Colour and pattern are also of rather limited use since it is often highly variable within species. The most recent subdivision of *Podarcis* was made by Klemmer (1957) who separated it into three assemblages.

1. *muralis*-group : *muralis, filfolensis, milensis, tiliguerta* and *wagleriana*.
2. *bocagei*(= *hispanica*)-group : *bocagei* (= *hispanica*), *lilfordi*, *pityusensis* and *dugesii*.*
3. *sicula*-group : *sicula, erhardii, melisellensis* and *taurica*.

Klemmer's classification produces zoogeographically coherent groups : one in the West (*hispanica*-group), another in the East (*sicula*-group) and the third (*muralis*-group) consisting of a single, widespread continental species, *P. muralis*, and four Mediterranean island forms, all occurring south of the main range of *P. muralis*, which are presumed to have originally been connected with it either directly as in the case of *P. milensis* and *P. tiliguerta* or via another member of the group : thus Klemmer believed that *P. wagleriana* and *P. filfolensis* are closest to *P. tiliguerta*.

However, many of the characters on which Klemmer's arrangement is based are rather equivocal and a wider range of evidence will be necessary to produce a convincing theory of *Podarcis* relationships. Chemotaxonomic studies may provide useful information (G. C. Ross and Arnold, in progress). But until this and other lines of evidence are adequately surveyed, it seems best to leave the question of *Podarcis* relationships open. Comment is limited here to two minor points.

1. Gross hemipenial structure often proves to be a good indicator of lacertid relationships. *P. hispanica* and *P. muralis* are alike in having the outer sulcal lips of the hemipenis free and differ from all other *Podarcis* in this respect. This may indicate that they are fairly closely related to each other. Such free lips are found in some of the members of *Lacerta* part II that may be related to the stock from which *Podarcis* was derived (see p. 355); so it is possible that *hispanica* and *muralis* are the most primitive members of *Podarcis* in this respect.

2. *P. erhardii* and *P. peloponnesiaca* seem to be closely related. Although quite distinct on the Greek mainland, where they have a small area of sympatry, the two species are to some extent connected by island populations of *P. erhardii* that approach *P. peloponnesiaca* in build and colouring. *P. peloponnesiaca* and most populations assigned to *P. erhardii* share a similar hemipenis shape in which the outer sulcal lips are broader than in other species of *Podarcis*.

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* As stated above, *L. dugesii* is here removed from *Podarcis*; Klemmer did not include *P. peloponnesiaca* in any of his assemblages because he was uncertain whether it was related to the rest of *Podarcis*.

The neighbouring *P. taurica* might also be close to these two species, especially as some island populations usually identified as *P. erhardii* approach *P. taurica* in form and colouring. Thus the *Podarcis* population on Skyros (N. Sporades) was originally named as a subspecies of *P. taurica* (*P. taurica gaigeae* Werner 1930) but is now usually referred to *P. erhardii*. Its hemipenial lips, however, are rather narrow and tend towards the condition found in *taurica*.

DISTRIBUTION (see Fig. 14). Mainly continuous including both highland and lowland areas but limited to the western part of the total region occupied by the West Palaearctic endemic genera dealt with in this paper. N.W. AFRICA (*P. hispanica* only) : Tunisia, N. Algeria, Morocco. MAINLAND EUROPE : All southern peninsulas and northwards to S. Netherlands, Rhine Valley, Bavaria, Czechoslovakia, Hungary and Roumania ; also Northwest Black Sea coast to Crimea (*P. taurica*) and N.W. Asia Minor (*P. muralis*). MEDITERRANEAN ISLANDS : Most islands with the exception of those lying east of a line running just west of Samothraki, Limnos, Agios Evstratios, Psara, Ikaria, Kos and Kasos in the Aegean Sea.

BIOLOGY. These small lizards occupy a relatively broad spectrum of spatial niches. Most are at least partly scansorial and some spend much of their time on semi-vertical surfaces (e.g. *P. muralis* and *P. hispanica*). Others (like *P. taurica*) climb relatively little.

PSAMMODROMUS Fitzinger

Fitzinger, 1826, *Neue Classif. Rept.* : 22.

TYPE SPECIES : *Psammodromus hispanicus* Fitzinger.

DIAGNOSIS. Small lacertids (adults usually under 80 mm snout to vent). Skull moderately built or robust, not depressed, a parietal foramen present, frontal bones paired throughout life ; postorbital and postfrontal bones fused even in hatchlings ; clavicle strongly expanded medially with a large always unemarginated foramen ; interclavicle cruciform, the lateral arms not directed strongly forwards or backwards ; sternal fontanelle oval ; sexual variation in presacral vertebral count present ; all presacral vertebrae, except first three cervicals, with ribs ; free ribs in two series, long anterior ones differentiated abruptly from short posterior ones ; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature ; lobes not folded in repose, regularly plicate with variable micro-ornamentation ; apical region of lobes short or quite long with small or moderately sized sulcal lips ; fairly large conical papillae sometimes present on lobe tips.

Head shields normal, nostril usually in contact with first upper labial and bordered posteriorly by a single postnasal scale ; lower eyelid scaly ; anteriorly parietal scale borders outer margin of fused postorbital–postfrontal bone ; supratemporal scales well developed ; masseteric shield not usually discernible.

Dorsal body-scales large, pointed, strongly keeled and overlapping ; collar absent or very weakly developed ; ventral scales smooth, truncate and overlapping, often strongly so, in six or ten longitudinal rows. Toes cylindrical or slightly compressed with smooth or keeled lamellae beneath; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern absent. Belly usually brightly coloured in breeding males.

SPECIES REFERRED. *algirus, blanci, hispanicus, microdactylus.*

SKELETAL FEATURES. Skull undepressed, robust with a thick osteodermal layer in *P. algirus*, less so in the other species. Supraocular lamellae complete in adults, temporal region ossified in *P. algirus*. Postorbital and postfrontal bones always fused, pterygoid teeth present only in *P. algirus*. Presacral vertebrae usually 26 or 27 in males, 27 or 28 in females (total range 26 to 29). Clavicle expanded medially, always unemarginated. Interclavicle cruciform, the lateral arms not obviously directed forwards. Sternal fontanelle oval. One pair of inscriptional ribs often present (but not usual in *P. hispanicus*). Non-autotomic caudal vertebrae four or five. Caudal pattern always C.

HEMIPENIS. Symmetrically bilobed without an obvious armature; lobes not folded in retracted organ, plicate. In *P. blanci*, *P. hispanicus* and *P. microdactylus* the apical parts of the lobes are short with quite large conical papillae at the tips and relatively small sulcal lips. *P. algirus* differs in having long apical sections to the lobes (twice as long as basal section) and the lobes themselves are slender with large lips that are free and expanded distally, and no conical apical papillae. Micro-ornamentation consists of simple recurved spines in *P. algirus* but in the other species the spines are irregular (and often bifurcated, Böhme 1971).

EXTERNAL FEATURES. Small lizards (adults usually 35 mm to 80 mm snout to vent). Nostril in contact with first upper labial, bordered posteriorly by a single postnasal. Eyelid scaly. Border of parietal shield unemarginated, usually running along outer margin of fused postorbital and postfrontal bones. Supratemporals well developed, the first often deepest in most species (last frequently deepest in *P. algirus*). Temporal scaling coarse, masseteric shield not clearly defined. Dorsal scales large (at least half the length of the proximal caudals), imbricate, strongly keeled and pointed. Number of dorsals in a transverse series 21 to 32. Collar very weak (*hispanicus*, some *blanci* and some *microdactylus*) or absent. Ventral plates smooth, truncate, strongly or extremely strongly imbricate (*P. algirus*), in six or ten* (*P. algirus*) longitudinal rows. Anal shield large, bordered by one or two rows of smaller plates. Toes not strongly compressed, tubercular beneath or with two series of keels (keeling strong in *P. hispanicus*, obtuse in some *P. microdactylus* and some *P. algirus*). Series of femoral pores extend to knee and consist of 10 to 21 pores in each. Tail unmodified, very long in *P. algirus*, as much as three times the snout–vent length.

COLORATION. Sexual dimorphism in dorsal pattern absent. Most individuals have light, narrow supraciliary and supralabial stripes extending along the body

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* In lacertids with large dorsal scales, it is often difficult to decide where these end and the equally large ventrals begin. But in forms with small dorsal scaling easily distinguished from the ventrals, the distribution of the latter corresponds closely with the *rectus abdominis superficialis* muscle. If this muscle is used as a criterion in defining the ventrals of *Psammodromus* species, it appears that *P. algirus* has ten longitudinal rows of ventrals rather than six as often stated (e.g. Boulenger 1921).

(these may be absent, especially in *P. blanci* and *P. microdactylus*). Other elements of the dorsal pattern rather variable. Venter brightly coloured in breeding males of the small species. *P. algirus* has a bright throat but a pale belly in breeding males.

RELATIONSHIPS. It is usually assumed that the three small species of *Psammodromus*, viz. *blanci, hispanicus* and *microdactylus*, are more closely related to each other than they are to *P. algirus*. This appears to be true ; *P. algirus* differs from them in several features including hemipenial structure, peculiar almost skink-like ventral scaling, extremely long tail and heavily armoured head. However, this species seems to be more closely related to the remainder of *Psammodromus* than it does to any other group of lacertids. The small species, *P. blanci* and *P. microdactylus*, appear to be very closely related and may even be conspecific.

DISTRIBUTION (see Fig. 15). N.W. AFRICA : Tunis, Algeria, Morocco. EUROPE : Spain, Portugal and southern France.

BIOLOGY. The three smaller species all typically occur in open areas often with low, dense vegetation in which they hunt and hide. *P. algirus* is often found in scrub regions, especially in the vicinity of bushes and shrubs. When disturbed, it retreats into the base of these and may sometimes climb in them.

GALLOTIA Boulenger

Boulenger, 1916, *Tr. Zool. Soc.* **21** : 3.

TYPE SPECIES : *Lacerta galloti* Duméril & Bibron.

DIAGNOSIS. Medium to large lacertids (adults of extant species up to 210 mm snout to vent). Skull robust, a parietal foramen present (not in the extinct *Lacerta* (= *Gallotia ?*) *maxima* according to Bravo 1953) ; frontal bones paired throughout life, postorbital and postfrontal bones fused, even in hatchlings ; clavicle strongly expanded medially, foramen always unemarginated ; interclavicle cruciform, the lateral arms not strongly directed forwards or backwards ; sternal fontanelle oval ; no sex correlated variation in presacral vertebral count ; all presacral vertebrae, except first three cervicals, with ribs ; free ribs in two series, long anterior ones differentiated from the short posterior ribs ; caudal vertebrae of the C pattern.

Hemipenis symmetrically bilobed with no obvious armature ; lobes not folded in repose, regularly plicate with micro-ornamentation of simple recurved spines. Apical regions of lobes usually fairly long, sulcal lips small, large conical papillae present on lobe tips.

Head shields normal, nostril in contact with first upper labial scute and bordered posteriorly by a single postnasal scale, eyelid scaly ; anteriorly parietal scute may or may not reach the outer margin of the fused postorbital and postfrontal bones ; supratemporals present, the anterior ones sometimes narrower than the rest ; a masseteric shield may be present.

Dorsal body-scales small or moderate sized (largest may be half the length of the proximal caudals) ; collar present and well defined ; ventral plates smooth, truncate, not strongly overlapping, in (8) 10 to 20 longitudinal rows. Toes not strongly compressed, tubercular beneath; femoral pores present. Tail long, unmodified. Sexual dimorphism in dorsal pattern usual. Belly brightly coloured at least in breeding males.

SPECIES REFERRED. *atlantica, galloti, simonyi.*

Perhaps also the extinct *Lacerta goliath* Mertens 1942 and *Lacerta maxima* Bravo 1953.

SKELETAL FEATURES. Skull robust, undepressed with thick osteodermal layer. Supraocular lamellae complete in mature specimens, temporal ossification present in *G. atlantica* and *G. simonyi simonyi*, much reduced or absent in *G. galloti* and *G. simonyi stehlini*. Postorbital and postfrontal bones fused throughout life, pterygoid teeth present. Almost unique in the family Lacertidae in having no sex-correlated variation in the number of presacral vertebrae there being 26 in nearly all the specimens examined (occasionally 25).

Clavicle expanded medially, always unemarginated. Interclavicle cruciform, the lateral arms not directed strongly forwards, although they may be swept slightly backwards in some *G. galloti*. Sternal fontanelle oval. Most frequently one well-developed pair of inscriptional ribs in *G. galloti* and *G. simonyi* but usually none in *G. atlantica*. In most cases five non-autotomic caudal vertebrae (sometimes four in *G. galloti* and *G. atlantica* and sometimes six in *G. simonyi*). Caudal pattern always C.

HEMIPENIS. Symmetrically bilobed without an obvious armature; lobes not folded in retracted organ, plicate. Apical sections of lobes longer than basal parts or approximately equal to them; lobe tips covered by prominent papillae which are conical, rather flattened and about equal in length to the widths of two to four plicae. Lips on lobe sulci relatively small, their free edges papillate. Micro-ornamentation consists of simple recurved spines.

EXTERNAL FEATURES. Medium to large lacertids (adults from about 60 mm to 210 mm snout to vent). Nostril in contact with first upper labial, bordered posteriorly by a single postnasal. Eyelid scaly. Border of parietal shield running along the outer edge of fused postorbital and postfrontal bones in *G. atlantica* and *G. galloti*, medial to this in *G. simonyi*. Supratemporals present, the first deep in *G. simonyi*, shallow in the other two species. A masseteric shield present in many *G. galloti* and *G. simonyi*, absent in *G. atlantica*. Dorsal scales very small (*G. galloti* and *G. simonyi*) or moderately large (*G. atlantica*), 45 to 110 in a transverse row across the mid-body, distinctly keeled, very strongly so in *G. atlantica*. Collar strong; serrated or smooth. Ventrals smooth, truncate, not very strongly imbricate, arranged in 10 (rarely 8) longitudinal rows in *G. atlantica*, 10 to 14 in *G. galloti* and 16 to 20 in *G. simonyi*. Preanal shield rather small, the scales in this region rather fragmented. Toes not strongly compressed, tubercular beneath. Femoral pores extend to knee, 17 to 33 in each series. Tail unmodified.

COLORATION. Sexual dimorphism in dorsal colouring of adults present in most populations. Young typically with two pairs of light, well defined flank stripes, one supraciliary, the other supralabial. These are usually separated and bordered by black pigment which may be either continuous or broken up. There may also be a light vertebral stripe and the pattern may be overlaid by irregular transverse rows of small white ocelli. The throat often bears a series of dark chevrons or is entirely dark. Females (and a few males of some forms) tend to retain the juvenile pattern of stripes although it may be fainter. In males (and some females, especially of *G. simonyi*) the dorsal coloration becomes more uniform (and in *G. galloti* and *G. simonyi* darker as well). Males (and females of *G. atlantica*) have prominent blue (*G. atlantica, G. galloti*) or yellow (*G. simonyi*) ocelli on the flanks and the outer ventrals are also often blue. In *G. g. galloti* the transverse rows of white ocelli on the back are also replaced by blue. The belly is also often brightly pigmented in adults although this colour is often largely obscured by melanin.

RELATIONSHIPS. In spite of considerable external differences, the three extant species of *Gallotia* appear to be relatively closely related to each other, albeit perhaps not as closely as the members of *Podarcis* or of *Lacerta* part I. It is generally assumed that the fossil forms discovered in Pleistocene deposits on the Canary Islands are also members of *Gallotia*. These have been found on some of the large islands in the western group (La Palma, Tenerife, perhaps Gomera) and have been named as *Lacerta* (*Gallotia*) *goliath* Mertens 1942 and *Lacerta* (*Gallotia*) *maxima* Bravo 1953. As indicated by their names, these fossil forms were larger than any extant species of lacertid, *L. maxima* having a skull length of over 120 mm and an estimated total length of 1200 mm (Bravo 1953). Insufficient data are available from the published descriptions to allow these giant forms to be firmly allocated to *Gallotia* but their skull shape and head scale impressions in the osteodermal layer resemble those of *G. simonyi*. If this indicates a real relationship, then this apparent species-group (i.e. *goliath, maxima* and *simonyi*) has undergone a considerable reduction in range. It does not now occur on La Palma, Tenerife or Gomera and has recently become extinct on Hierro and the nearby Roques Zalmor (Klemmer, personal communication) where it was represented by *G. simonyi simonyi*. The only known population remaining is on Gran Canaria (*G. simonyi stehlini*). On all the islands where the lizards of the putative *simonyi*-group have disappeared, *G. galloti* now exists. Possibly competitive exclusion by this species has been important in bringing about the extermination of the *simonyi*-group on some islands but it is uncertain if this was the case on Hierro. Here *G. simonyi* was represented by a very large-bodied population (adults up to 210 mm snout to vent) while the resident race of *G. galloti* (*G. galloti caesaris* (Lehrs)) is much smaller (less than 100 mm snout to vent) which suggests that the two forms were unlikely to compete directly, unless of course there was competition between the young *simonyi* and the adult *galloti*.

The three species definitely assigned to *Gallotia* have no very close relationship to the lizards assigned to *Lacerta* part I. The affinities of *Lacerta lepida* which was previously placed in *Gallotia* by Peters are discussed on p. 333.

DISTRIBUTION (see Fig. 15). Restricted to the Canary Islands.

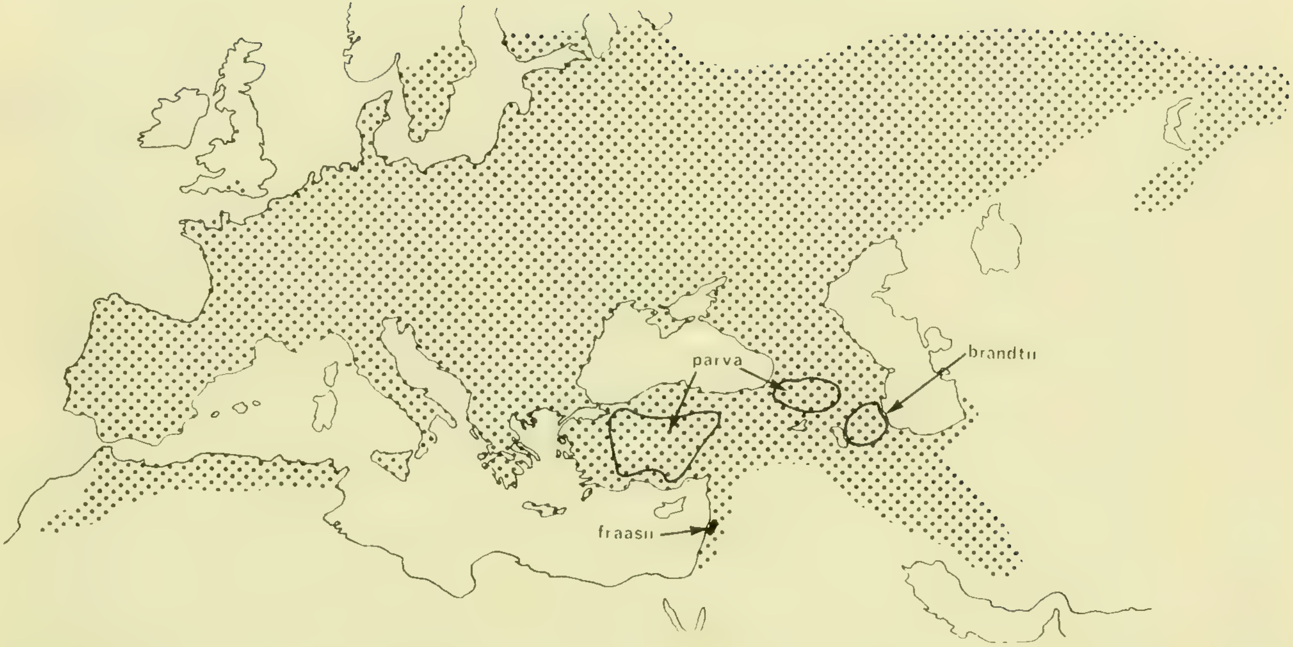
parva
brandtii
fraasii

FIG. 12. Distribution of *Lacerta* part I and the *L. parva*-group of *Lacerta* part II. Stippling: approximate distribution of *Lacerta* part I. Enclosed areas: approximate distribution of the *L. parva* species group.

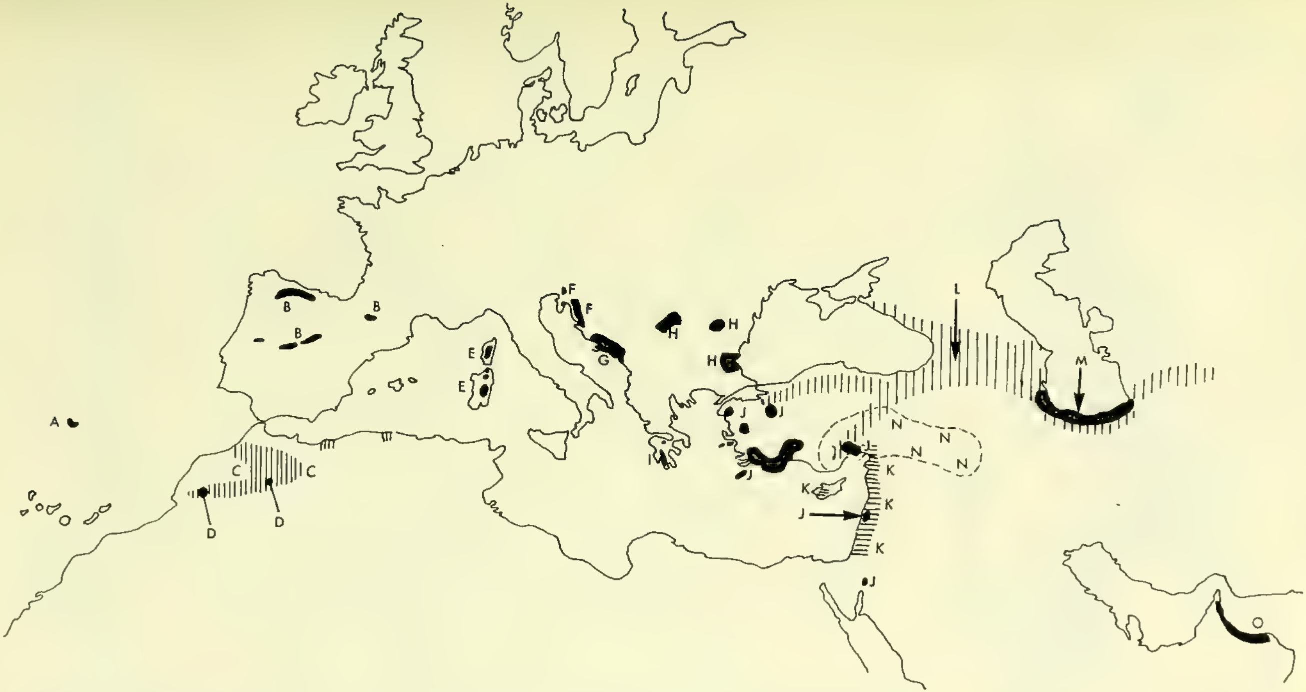

FIG. 13. Distribution of *Lacerta* part II excluding *L. vivipara* and the *L. parva* species-group. A: *L. dugesii*. B: *L. monticola*. C: *L. perspicillata*. D: *L. andreanszkyi*. E: *L. bedriagae*. F: *L. horvathi*. G: *L. mosorensis* and *L. oxycephala*. H: western populations of *L. praticola*. I: *L. graeca*. J: *L. danfordi*. K: *L. laevis*. L: *L. saxicola* group of species; *L. saxicola* occurs over whole area but the following are confined to the general region of the Caucasus: *L. armeniaca, L. caucasica, L. dahli, L. derjugini,* eastern populations of *L. praticola, L. rostombekovi, L. rudis* and *L. unisexualis*. M: *L. chlorogaster*. N: *L. cappadocica*. O: *L. cyanura* and *L. jayakari*. (*See* Fig. 1 for *L. vivipara* and Fig. 12 for the *L. parva* species-group.)

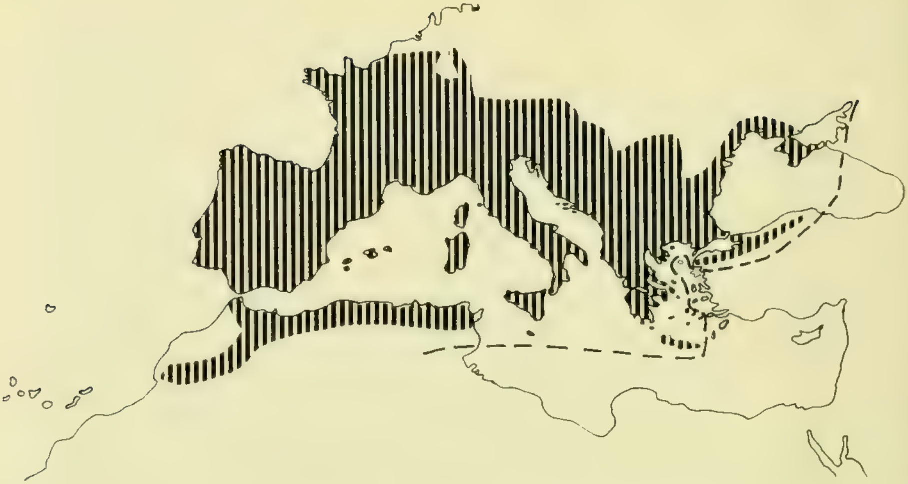

FIG. 14. Distribution of *Podarcis*. Broken line indicates eastern limit of the genus.

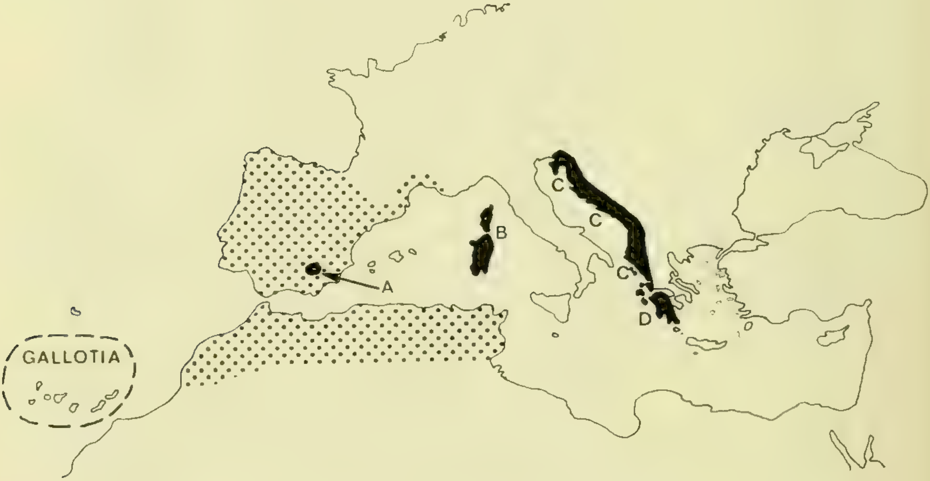

FIG. 15. Distribution of *Algyroides*, *Psammodromus* and *Gallotia*. Black: range of *Algyroides* (A = *A. marchi*, B = *A. fitzingeri*, C = *A. nigropunctatus*, D = *A. moreoticus*). Stipple: range of *Psammodromus*. Broken line: range of *Gallotia*.

BIOLOGY. The lizards of the genus *Gallotia* are among the largest terrestrial vertebrates native to the Canary Islands. The eastern *G. atlantica* is partly scansorial and feeds mainly on small invertebrates, while the western *G. galloti* and *G. simonyi* climb less and eat a substantial amount of vegetable food (see, e.g., Krefft 1950). These vegetarian habits are sometimes attributed to the lack of small animal prey on the islands (e.g. Peters 1961) but it may be more likely that these lizards have partly occupied plant-eating niches because, in the depauperate fauna of the Canaries, these are not completely filled by more efficient herbivores.

The species of *Gallotia* tend to produce small clutches of eggs (usually 1 to 3 – Krefft 1950) for their size. This compares with broods of 8 to 18 in species of *Lacerta* part I of equal body size (Peters 1961).

RELATIONSHIPS OF *ALGYROIDES, LACERTA, PODARCIS, PSAMMODROMUS* AND *GALLOTIA*

The fossil record of the Lacertidae is far too fragmentary to give any useful information about relationships within the family, so all speculation about this must be based very tentatively on comparisons of extant forms. If the groups of lizards discussed in this paper are compared with the rest of the Lacertidae, it is apparent that *Lacerta* part II has more features that are widespread in the Lacertidae as a whole than the other groups (see Table IV). *Lacerta* part II is a very varied assemblage with many, often well-differentiated species and has a complex relict distribution. These features suggest that it is long established. It could be argued from this and its greater resemblance to the rest of the family that *Lacerta* part II might be closest to the stock which gave rise to the endemic West Palaearctic group of genera. Such a conclusion is of course highly provisional.

Lacerta part I is morphologically very like *Lacerta* part II and is separated partly because its members have a close and detailed resemblance to each other; the actual common features that divide the species of part I from part II are relatively slight (large body-size, dorsal pattern, no bright belly colour, distinctive type of ecological niche) and it seems probable that they are a relatively recent offshoot of *Lacerta* part II although it is not possible to suggest at present what part of this assemblage gave rise to them. Comparatively recent origin, or at least recent expansion, is also suggested by the close similarity of the species in *Lacerta* part I and their continuous distribution.

Similarly *Algyroides* is also close to *Lacerta* part II, being differentiated only by large dorsal scales and to some extent by the very small size of the sulcal lips on the hemipenial lobes. This group appears to have most features in common with the more typical members of *Lacerta* part II.

In the case of the genus *Podarcis*, homogeneity and continuous (and relatively small) range indicate recent origin or expansion. Most of the characters that in combination distinguish its members occur sporadically in *Lacerta* part II, more particularly in *L. danfordi* and its closer relations, viz. *L. laevis*, *L. graeca* and the southwestern species – *L. andreanszkyi*, *L. dugesii* and *L. perspicillata*. Among these characters are large apical sections to the hemipenial lobes (*danfordi*) and

TABLE IV: Distribution of features widespread in the rest of the Lacertidae

Feature	Approximate incidence in Lacertidae excluding West Palaearctic endemic genera	*Lacerta* part I	*Lacerta* part II	*Algyroides*	*Podarcis*	*Psammodromus*	*Gallotia*
Postorbital and postfrontal bones unfused in hatchlings	Over 60% of species	+ (exception)	+ (exception)	+	+	–	–
Sexual variation in pre-sacral vertebral number	All, except a few *Acanthodactylus* spp.	+	+	+	+	+	–
A-type caudal vertebral pattern	Over 70% of species	Some individuals	Some individuals	Some individuals	–	–	–
Hemipenis with distinct armature	Over 80% of species	–	Some	–	–	–	–
Two superposed postnasals	80% of species	+ (exceptions)	+/–	+ (exceptions)	– (exceptions)	–	–
Margin of parietal shield does not reach edge of bony parietal table	80% to 90% of species	+	+ (exceptions)	+	–	–	+/–
Sexual dimorphism in dorsal pattern absent	Most forms	– (exceptions)	+ (exceptions)	+ (exception)	– (few exceptions)	+	–

extremely well-developed sulcal lips (*danfordi, andreanszkyi*), hemipenial micro-ornamentation of simple spines (*graeca* and the southwestern species group), C-type caudal vertebrae (some *danfordi*), sternal fontanelle approaching cordiform shape (*andreanszkyi, laevis, danfordi*), parietal shield margin reaching outer edge of postorbital bone (southwestern species group), well-developed masseteric shield in some cases (*andreanszkyi, laevis*), *Podarcis*-type dorsal pattern (*andreanszkyi*). In spite of the above individual peculiarities, all these species are closer to other members of *Lacerta* part II than they are to *Podarcis*.

Of the species cited above, *L. andreanszkyi* appears to have more in common with *Podarcis* than the others, and it may be closest to the stock that gave rise to the genus. This tentative hypothesis receives some support from the fact that one species of *Podarcis*, *P. hispanica*, can be quite similar in appearance to *L. andreanszkyi*, especially in the Atlas of Morocco where both of these forms occur. As stated (p. 346), there are reasons for believing that *P. hispanica* may be one of the more primitive members of *Podarcis*.

Boulenger (1921) thought that *Psammodromus* might be related to *Lacerta parva*. Certainly, there is an external resemblance between the smaller species of *Psammodromus* and this form that extends to habitus, scale-shape and coloration, although this could be convergent as these lizards occupy similar habitats. *L. parva* resembles the small *Psammodromus* species in having a rather similar, peculiar pattern of hemipenial micro-ornamentation (Böhme 1971) ; also its caudal vertebrae approach the C type. However, there are a number of important differences between *L. parva* and *Psammodromus* ; the latter lacks the following features that occur in *L. parva*, viz. postorbitals and postfrontals unfused, double postnasals, reduced chromosomal formula and lack of plicae on hemipenial lobes. It appears unlikely therefore that there is a very close connexion between *Psammodromus* and *L. parva* although the former may well be derived from *Lacerta* part II.

Gallotia is usually said to be closely related to *Lacerta* part I (e.g. Boulenger 1920, Peters 1961) but the two groups show many points of difference and the closest relatives of *Gallotia* appear to be the small species of *Psammodromus*. Although the more extreme forms of these two groups are superficially very different, they have many similarities especially in skeleton and hemipenis. The smallest species of *Gallotia*, *G. atlantica*, has large dorsal scales approaching those of *Psammodromus* in relative size.

SUMMARY OF PROPOSED SYSTEMATIC CHANGES

Algyroides Bibron & Bory

This genus is limited to the four European species, viz. *fitzingeri* (Wiegmann 1834), *marchi* Valverde 1958, *moreoticus* Bibron & Bory 1833 and *nigropunctatus* (Duméril & Bibron 1839). The three African species originally placed in *Algyroides* are now placed in *Adolfus* Sternfeld 1912 ; these are *africanus* Boulenger 1906, *alleni* Barbour 1914 and *vaueresellі* (Tornier 1902).

Lacerta Linnaeus 1758

The central and southern African species, viz. *australis* Hewitt 1926, *echinata* Cope 1862, *jacksoni* Boulenger 1899 and *rupicola* Fitzsimons 1933, are not considered to be congeneric with the Palaearctic species of *Lacerta*. Their affinities lie with other Ethiopian lacertids and will be discussed more fully elsewhere. *L. echinata* and *L. jacksoni* are related to the Central African species placed in *Adolfus*, *Bedriagaia* and *Gastropholis* ; *L. rupicola* is perhaps related to *Tropidosaura* ; and the precise affinities of *L. australis* are unknown, as the type cannot be found.

Palaearctic *Lacerta*, as usually understood (and including *L. cappadocica* Werner 1902) is divided into three main groups two of which are here raised to the status of independent genera. Species are allocated as follows.

Podarcis Wagler 1830, including *erhardii* Bedriaga 1882, *filfolensis* Bedriaga 1876, *hispanica* Steindachner 1870, *lilfordi* (Gunther 1874), *melisellensis* Braun 1877, *milensis* Bedriaga 1882, *muralis* (Laurenti 1768), *peloponnesiaca* Bibron & Bory 1833, *pityusensis* Bosca 1883, *sicula* Rafinesque 1810, *taurica* Pallas 1814, *tiliguerta* Gmelin 1789, *wagleriana* Gistel 1868.

Gallotia Boulenger 1916, including *atlantica* Peters & Doria 1882, *galloti* Duméril & Bibron 1839, *simonyi* Steindachner 1889.

The remaining species are left in *Lacerta* but this is divided into two parts : *Lacerta* part I and *Lacerta* part II.

Lacerta part I contains the following species : *agilis* Linnaeus 1758, *lepida* Daudin 1802, *princeps* Blanford 1874, *schreiberi* Bedriaga 1878, *strigata* Eichwald 1831, *trilineata* Bedriaga 1886, *viridis* (Laurenti 1768).

Lacerta part II contains all other species presently assigned to *Lacerta*.

Psammodromus Fitzinger 1826

This genus is not changed and contains the four species *algirus* (Linnaeus) 1758, *blanci* (Lataste 1880), *hispanicus* Fitzinger 1826, *microdactylus* (Boettger 1881).

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APPENDIX I: RELATIONSHIPS OF THE AFRICAN SPECIES OF *ALGYROIDES*

Three Central African species of lacertid are usually placed in *Algyroides*, namely *A. africanus* Boulenger 1906, *A. alleni* Barbour 1914 and *A. vauereselli* (Tornier 1902). *A. africanus* was the first African species to be assigned to *Algyroides*. When he described it, Boulenger was struck by the superficial resemblance of this species to the European *A. nigropunctatus* and had no hesitation about regarding them as congeneric. The other African forms are much less like the European members of *Algyroides* but have fairly obvious affinities to *A. africanus*. When the two geographical groups are compared in detail it becomes apparent that they are not very similar ; the principal differences are listed below.

	European species	*African species*
1 Postnasals	Usually two	One
2 Masseteric shield	Usually present	Always absent
3 Edge of parietal shield	Does not border outer edge of postorbital bone	Borders outer edge of fused postorbital–postfrontal bones
4 Parietal foramen	Present	Absent
5 Postorbital and postfrontal bones fused	No	Yes
6 Clavicle	Strongly expanded medially, posterior margin of foramen slender, emarginated in some individuals of all species	Unexpanded (except in *A. vauereselli* where the posterior margin is very thick) ; never emarginated
7 Caudal vertebrae	Usually B pattern	Always A pattern
8 Hemipenial armature	Absent	Present
9 Lobes of retracted hemipenis complexly folded	No	Yes

All the features present in the four European species occur widely in Palaearctic *Lacerta* and many of them are found in *Podarcis*, *Psammodromus* and *Gallotia* too. The characters typical of the African species group occur in combination in a number of other Equatorial lacertid species (viz. *Bedriagaia tropidopholis*, *Gastropholis prasinus*, *G. vittatus*, '*Lacerta*' *jacksoni* and '*Lacerta*' *echinata*). It seems likely therefore that the superficial resemblance between *A. africanus* and *A. nigropunctatus* is a convergent one (perhaps connected with the similar requirements of their original woodland or woodland-edge habitats), and that the European and African members of the genus are unrelated. Thus the name *Algyroides* must be restricted to the European forms and another one found for the African ones ; *Adolfus* Sternfeld 1912 is available.

APPENDIX II: MATERIAL EXAMINED

Figures in parentheses indicate number of specimens examined. The first figure denotes those investigated for osteological characters by radiography or alizarin preparation, the second figure the number of hemipenes examined.

LACERTA part I

agilis (47 ; 7), *lepida* (17 ; 8), *princeps* (3 ; 1), *schreiberi* (16 ; 3), *strigata* (11 ; 3), *trilineata* (19 ; 6), *viridis* (24 ; 6).

LACERTA part II

andreanszkyi (9 ; 2), *armeniaca* (5 ; –), *bedriagae* (25 ; 5), *brandtii* (11 ; 3), *cappadocica* (13 ; 5), *caucasica* (9 ; 3), *chlorogaster* (20 ; 3), *cyanura* (3 ; 1), *danfordi* (16 ; 7), *derjugini* (9 ; 3), *dugesii* (36 ; 8), *fraasii* (6 ; 2), *graeca* (10 ; 6), *horvathi* (21 ; 5), *jayakari* (14 ; 2), *laevis* (26 ; 4), *monticola* (25 ; 4), *mosorensis* (19 ; 6), *oxycephala* (28 ; 8), *parva* (17 ; 4), *perspicillata* (22 ; 6), *praticola* (18 ; 3), *rudis* (7 ; 2), *saxicola* (21 ; 6), *vivipara* (24 ; 7).

ALGYROIDES

fitzingeri (21 ; 2), *marchi* (10 ; 2), *moreoticus* (14 ; 3), *nigropunctatus* (18 ; 6).

PODARCIS

erhardii (45 ; 6), *filfolensis* (25 ; 2), *hispanica* (36 ; 6), *lilfordi* (20 ; 6), *melisellensis* (28 ; 5), *milensis* (11 ; 5), *muralis* (40 ; 10), *peloponnesiaca* (20 ; 4), *pityusensis* (17 ; 4), *sicula* (23 ; 6), *taurica* (23 ; 7), *tiliguerta* (21 ; 4), *wagleriana* (27 ; 3).

PSAMMODROMUS

blanci (6 ; 2), *hispanicus* (17 ; 3), *microdactylus* (11 ; 2).
algirus (25 ; 5).

GALLOTIA

atlantica (25 ; 6), *galloti* (35 ; 6), *simonyi* (27 ; 3).

ADOLFUS (i.e. Central African species customarily assigned to *Algyroides*)

africanus (17 ; 4), *alleni* (32 ; 6), *vauereselli* (4 ; 2).

APPENDIX III: VARIATIONS IN PRESACRAL NUMBER

The figures below are based on the material listed in Appendix II. Although, where possible, samples include individuals from different parts of the range of the species concerned, they are not large enough to give a complete picture of variation in presacral vertebral count. **Bold** figures indicate commonest numbers for each species.

	Males						*Females*					
	24	25	26	27	28	29	25	26	27	28	29	30
LACERTA **part I**												
agilis			2	6	6					8	**23**	1
lepida				**11**	1					**5**		
princeps				1						1	1	
schreiberi				**7**	1				1	**7**		
strigata				**6**						**8**	1	
trilineata				**9**	1					**8**	1	
viridis			1	**7**	2				2	**7**	2	
LACERTA **part II**												
andreanszkyi			1	1	1					1	4	
armeniaca											**5**	
bedriagae		1	**12**	1				4	**7**			
brandtii			**4**					1	**5**	1		
cappadocica		1	**4**						**7**			
caucasica			1	**6**						2		
chlorogaster			1	**16**	1					3		
cyanura								2				
danfordi			**6**	1					**9**			
derjugini			**4**						1	**3**	1	
dugesii		2	**25**					8	**13**			
fraasii				1	**2**						**3**	
graeca			1	**5**					2	1		
horvathi			**5**						**13**	2		
jayakari		**10**						**4**				
laevis		1	**15**					2	**6**	1		
monticola		1	**10**					1	**7**	5	1	
mosorensis			**9**	5					**6**	1		
oxycephala		**9**	3					**12**				
parva				4	**6**	1				2	**4**	
perspicillata			4	4					4	**10**		
praticola			1	**8**	2				1	1	2	1
rudis				**3**						**3**	1	
saxicola				**8**	2				2	3	**6**	
vivipara		3	**8**	1					4	6	1	
ALGYROIDES												
fitzingeri			**9**						**5**	1		
marchi		**8**						2				
moreoticus	1	6	3	1				1	**4**	1		
nigropunctatus	1	**10**					1	**5**				

	Males						*Females*					
	24	25	26	27	28	29	25	26	27	28	29	30
PODARCIS												
erhardii				**16**	8					**10**	5	
filfolensis		1	**15**						**9**			
hispanica			**9**	**9**	1			1	4	**8**	3	
lilfordi			4	3	1				**7**			
melisellensis				**16**					1	**9**	2	
milensis				**9**						**9**		
muralis			13	**9**					1	**6**	1	
peloponnesiaca				12						**8**		
pityusensis		1	**8**	1				2	**3**	1		
sicula			4	**11**					2	4	2	
taurica				**14**	1				1	**4**	3	
tiliguerta		2	**10**						**17**		1	
wagleriana			1	**11**	1					**13**	1	
PSAMMODROMUS												
algirus			**10**	1					**11**	3		
blanci			2							**4**		
hispanicus			**6**						2	**8**	1	
microdactylus			**6**							**5**		
GALLOTIA												
atlantica			**12**					**13**				
galloti		1	**17**					**17**				
simonyi			**15**				2	**10**				

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DISTRIBUTION, ECOLOGY AND EVOLUTION OF THE BELLBIRDS (*PROCNIAS*, COTINGIDAE)

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D. W. SNOW

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DISTRIBUTION, ECOLOGY AND EVOLUTION OF THE BELLBIRDS (*PROCNIAS*, COTINGIDAE)

By D. W. SNOW

THE four species of bellbirds of the genus *Procnias* constitute one of the most peculiar of the many isolated genera placed in the suboscine family Cotingidae. This New World family, of mainly tropical distribution, is so diverse that it might well be subdivided into several families if there appeared to be any reasonable way of doing so. The recent studies of Ames (1971) and Olson (1971) show, however, that the anatomical characters that have been used to distinguish the higher categories of suboscine birds are distributed in a most confusing pattern among the cotingid genera, and it would be premature to attempt a full revision at the higher systematic levels until a better understanding of these and other characters has been attained. It is at least clear that many of the cotingid genera are of ancient origin, though it is not known whether the modern genera are a remnant of a much greater variety of forms, of which many have become extinct, or whether the evolution of the family has been concentrated along those phyletic lines which are still alive today.

In a family consisting largely of frugivorous forest birds, the bellbirds are perhaps the most specialized fruit-eaters of all. The only detailed field study, of *Procnias averano* in Trinidad (Snow 1970), showed that the adults not only feed entirely on fruit themselves but feed the young on fruit alone. They have short bills, very broad at the gape, which give the head an almost frog-like appearance and enable them to swallow whole relatively very large fruits. In this respect they are closely paralleled by the broadbill genus *Calyptomena* (Eurylaimidae) of the oriental region (Olson 1971), while the other medium-sized fruit-eating cotingas (e.g. *Cotinga, Xipholena*) show this beak form in less extreme degree. Like other cotingas, bellbirds typically pluck their food in flight.

In common with some other fruit-eating forest cotingas – and in parallel with the birds of paradise (Paradisaeidae) of the New Guinea region – the bellbirds have evolved extreme sexual dimorphism. The males of the four species are superficially very distinct, being ornamented in strikingly different ways with wattles or bare areas of skin. Two of them are among the very few species of land-birds with wholly white plumage. The females, on the other hand, are very alike, being olive-green above and pale yellowish with longitudinal streaks below. They are considerably smaller than the males – 85–89 per cent by wing-length, and about 71 per cent by weight in *P. nudicollis*, the only species for which an adequate series of weights is available (Table 1). The males spend much of their time in epigamic display, making themselves conspicuous by uttering extraordinarily loud explosive calls from high perches. At close quarters, visual displays are combined with calls. Snow (1970) gives a detailed account of the behaviour of the Bearded Bellbird, *P. averano*, and short accounts of *P. alba* and *P. tricarunculata* have been given by Snow (1961) and Skutch (1969) respectively.

TABLE 1

Wing-measurements of males and females of the four species of *Procnias*

		N	Range	Mean
P. averano	adult males	8	152–163	158·5
	immature males	9	146–161	155·0
	females	6	133–142	138·3
P. nudicollis	adult males	24	151–164	156·7
	immature males	51	144–162	154·0
	females	41	130–149	139·1
P. alba	adult males	13	155–170	161·0
	immature males	6	156–163	160·0
	females	11	131–140	136·4
P. tricarunculata	adult males	39	160–175	165·5
	immature males	16	155–171	163·4
	females	13	136–152	145·1

Notes. Measurements of *P. averano* are for the Venezuelan and Trinidad population; N.E. Brazilian birds apparently do not differ appreciably in size.

Sexing of birds in female plumage is sometimes unreliable in the older collections. One specimen of *P. alba*, labelled female, with a wing of 159 mm is omitted since it is almost certainly wrongly sexed.

Weights of *P. nudicollis*: 3 adult males, 177–225 g (average 199); 5 immature males 168–201 g (average, 184); 5 females, 120–150 g (average, 142).

The complete synonymy of the genus, with all previous important literature citations and distributional records, was given by Hellmayr (1929), since when no new form has been described and no major extension of range recorded.

RELATIONSHIPS WITHIN THE GENUS

The four species are illustrated in Figure 1. This drawing shows the conspicuous differences between the species, but does not indicate the less conspicuous resemblances between them, on the basis of which it is fairly clear that they fall into two closely related pairs, *P. averano* and *P. nudicollis* on the one hand and *P. alba* and *P. tricarunculata* on the other. Each of these pairs has a number of characters in common, and there is little doubt that the genus in its present state has arisen from an original splitting of an ancestral form into two species, followed by a further splitting of each.

P. averano and *P. nudicollis.* In the adult male the throat is bare or furnished with rudimentary black feathers ; there is a bare patch of skin on the side of the femur ; and the modified tips of the outer primaries (Figure 2) are somewhat

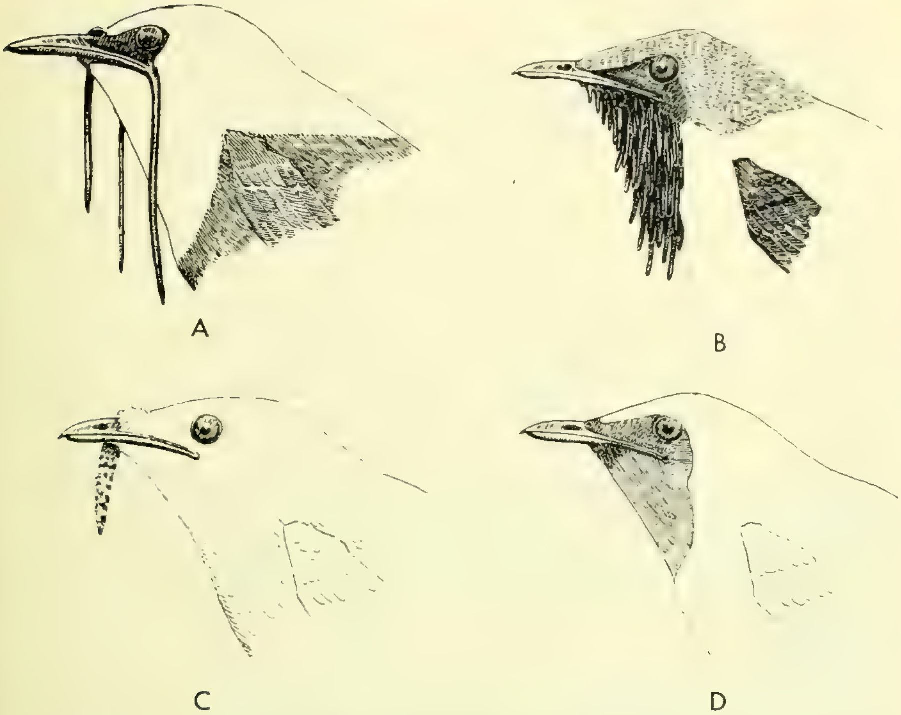

FIG. 1. Adult males of (A) *Procnias tricarunculata*, (B) *P. averano*, (C) *P. alba*, (D) *P. nudicollis*. Colour of plumage as follows: *P. tricarunculata*, head white, rest of plumage chestnut brown; *P. alba* and *P. nudicollis*, all white (bare skin of face and throat greenish in *P. nudicollis*); *P. averano*, top of head coffee-brown, wings black, rest of plumage very pale grey in western population, white in northeastern Brazilian population.

alike. In the juvenile male, the crown passes through an intermediate sooty-black stage before it acquires the adult colour. In the adult female, the crown is darker than the back and the throat feathers are mainly dark. These two species are almost exactly the same size, and a little smaller than the other two (Table 1).

In both species the males have two distinct kinds of call: a single short hammer-like note, and a succession of less loud, regularly repeated notes.

P. alba and *P. tricarunculata*. The adult males of both species have an elongated wattle springing from the base of the upper mandible (*P. tricarunculata* also has two similar wattles arising from the corners of the gape); the throat is feathered; there is apparently no bare patch on the femur; and the modified tips of the outer primaries are much alike in shape. The juvenile male does not develop a dark crown at any stage. In the adult female, the crown is the same green as the back and the throat is pale.

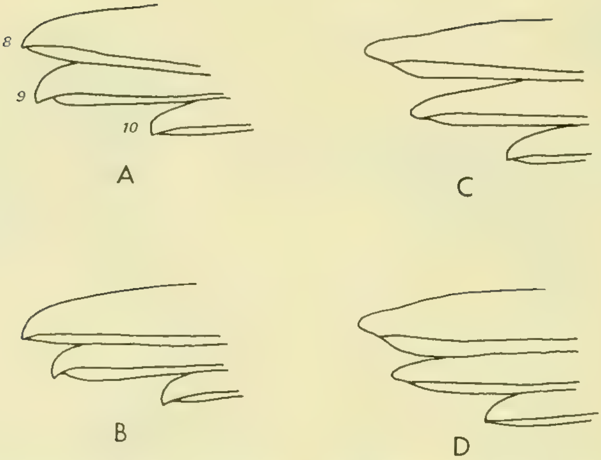

FIG. 2. Shapes of outer primary feathers in adult males of the four species of *Procnias*. (A) *P. tricarunculata*; (B) *P. alba*; (C) *P. averano*; (D) *P. nudicollis*. The three outermost primaries of the right wing are shown. Note that not only does the shape of the feather tip agree in *P. tricarunculata* and *P. alba*, and in *P. averano* and *P. nudicollis*, but also the ninth primary is the most modified in the first pair, and the eighth primary in the second pair. There is some individual variation in the degree of modification of the feathers.

The calls of the males are alike in so far as both have a disyllabic call of which the second note is slightly higher-pitched than the first.

DISTRIBUTIONAL HISTORY

All four species have an essentially montane distribution. *P. nudicollis* and *P. tricarunculata*, living at the highest latitudes, undertake extensive vertical migrations, breeding in montane forest and descending to lowland forest in the off-season. *P. alba* and *P. averano* wander to some extent, perhaps regularly, from the montane areas which are their headquarters, for in spite of comparatively little collecting and rare field observation there are a number of records of undoubted stragglers (Figure 3). The montane distribution, and the complete absence of the genus from the Andes, except for the eastern spur of the range in Venezuela and extreme eastern Colombia, strongly suggest that the genus originated in highland forest of the Guiana shield or some part of eastern Brazil.

Figure 3 shows the present distribution of the genus, so far as known. It is rather unlikely that further collecting will substantially modify the picture, except perhaps in the area where the ranges of *P. alba* and *P. averano* meet (see below); indeed it is unfortunately more likely that with the deforestation of eastern Brazil and Central America *P. nudicollis* and *P. tricarunculata* no longer exist in many areas where they formerly occurred, while the survival of the eastern population of *P. averano* is gravely threatened, if indeed it still exists (see notes to Figure 3).

If the relationships of the species are as suggested in the preceding section, it is likely that the original split was into an eastern and a western form. The subsequent split of each daughter-form into two species must have involved extensions of ranges and possibly also interactions between the products of the original split. Any reconstruction is of course highly speculative, but the following is suggested as the most likely (Figure 4).

The original split probably gave rise to two stocks, one in eastern Brazil and the other in the Guiana highlands. This is based on the fact that three of the four species occur in northern and eastern parts of South America ; while the presence of an isolated species in Central America and the complete absence of the genus from the main chain of the Andes (a unique distribution in the Cotingidae) strongly suggest that the Central American population reached its present home by long-range colonization.

The eastern form probably split into two – *averano* in the north, *nudicollis* in the south – during a period of aridity, when the highland forests of northeastern Brazil were isolated (as they now are) from those of eastern coastal Brazil. The western form, as already suggested, meanwhile probably split into two by establishing an isolated offshoot in Central America. The result of these processes would have been a chain of four species arranged in a phylogenetically 'logical' order from east to west.

The present distribution, however, is not so simple. *P. averano* has two widely separated populations, with *P. alba* interposed between them in the Guiana highlands, where on the present hypothesis it is likely to have originated. One may suppose that the western population of *P. averano* reached its present area by a long-range colonization from the east ; and this may well have been very recent, since the eastern and western forms constitute only slightly marked subspecies. Further support for this interpretation is derived from the fact that the Venezuelan north coastal mountains have clearly not been an evolutionary centre of any importance in the Cotingidae ; no species has its centre of distribution in this area, in marked contrast to the Guiana highlands and eastern Brazil.

The suggestion put forward by Snethlage (1928 : 539), that the present distribution of *P. averano* north and south of the Amazonian lowland forest indicates that at some time in the past dry savanna woodland was continuous across what is now the lower Amazon valley, seems much less likely. He was impressed by the occurrence of *P. averano* in rather dry, highly seasonal forest in northeastern Brazil ; but this is not generally typical of the habitat of bellbirds, and it seems more likely that, in the area where it still occurs in northeastern Brazil, *P. averano* is restricted to the richest montane forest which remains, the whole of this part of the continent having probably suffered from recent desiccation.

There remains the problem of the present relationship between *P. alba* and *P. averano* in the area where they adjoin. Phelps & Phelps (1963) give the altitudinal range of *P. alba* in Venezuela as tropical, up to 1000 m, and that of *P. averano* as tropical and lower subtropical, from 360 to 1600 m. The altitudes given for *P. averano*, however, include the north coastal mountains, where *P. alba* does not occur. In the southeast of the country, where the two species meet, there is only slight

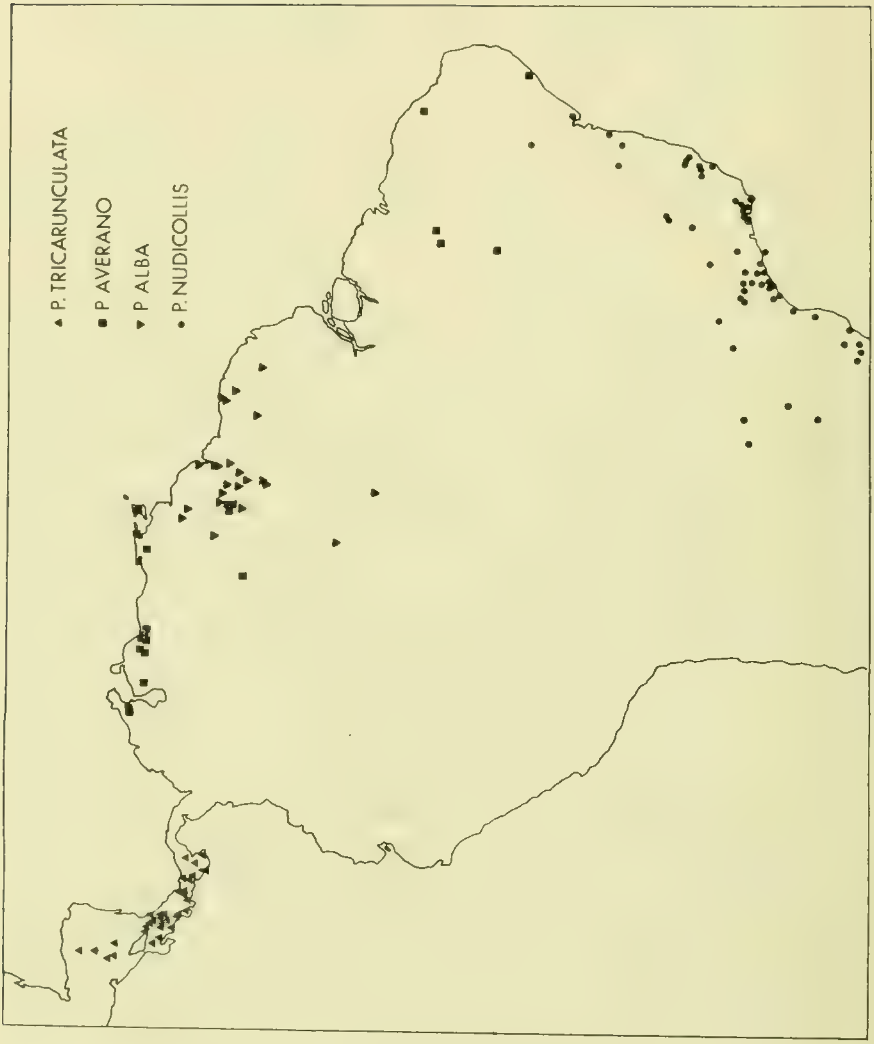
▲ P. TRICARUNCULATA
■ P AVERANO
▼ P ALBA
● P. NUDICOLLIS

FIG. 3. Distribution of the genus *Procnias*.

evidence that they differ in altitudinal preference ; but the data are so fragmentary that further collecting or observation may well alter the picture, and it may even turn out that on Roraima and perhaps other mountains *P. alba* occurs at low altitudes and is replaced at higher altitudes by *P. averano*. The records available at present are as follows :

Procnias alba		*Procnias averano*	
Roraima	1100 m	Roraima	1100–1300 m
Auyan-tepui	1100–1500 m	Acopan-tepui	1200–1600 m
Cerro Tomasote	500–600 m	Uei-tepui	1300 m
Altiplanicie de Nuria	460 m	Maniña head-waters	700 m

If, as suggested above, *P. averano* 'leap-frogged' over *P. alba* to establish itself in the coastal mountains of Venezuela, subsequent expansion of the newly established population would have brought it into contact with *alba* in the east. That they now apparently replace each other with little or no overlap, in spite of the fact that individuals must frequently straggle into each other's range, strongly suggests that they are ecologically or ethologically incompatible. The two are nearly the same size and feed in the same way, so that the usually accepted conditions for competition exist ; but it is not easy to see how competition for food could operate, when many other species share all of their foods, which are probably often, perhaps usually, locally superabundant (Snow 1971). The possibility of behavioural interactions unconnected with food supply should be borne in mind.

FIG. 3

Sources and notes.

P. tricarunculata. Records from Hellmayr (1929) Slud (1964) and Monroe (1968), supplemented by specimens in museums of Paris, New York, Washington, Yale and Philadelphia. Not all records can be shown in Panama and Costa Rica, but the limiting records are shown.

P. averano. Records from Hellmayr (1929), Pinto (1944, 1954), Meyer de Schauensee (1950), Camargo (1957), Phelps & Phelps (1962, 1963) and specimens in U.S. National Museum, Washington. The species just extends to Colombia (Montes de Oca, Colombia–Venezuela border) and to Brazil (Cotinga River and Cerro Uei-tepui (El Sol) on the Venezuelan border). The only record from Guyana based on a specimen (Adaroo River, Phelps coll.) is omitted, as the locality is untraceable. A sight record from Guyana (Kanuku Mountains, within the range of *P. alba*, March 1970; pers. obs.) is also omitted.

For the northeastern population the records plotted represent all that are known, except for the original specimen collected in Pernambuco, without exact locality, by Marcgrave (Pinto 1944).

P. alba. Records from Hellmayr (1929), Haverschmidt (1955, 1968), Phelps & Phelps (1963) and Snyder (1966). The two far southerly records (Barcelos and 20 miles up the Rio Negro from Manaos) almost certainly refer to stragglers. Occasional stragglers (not shown) have also occurred in Trinidad, within the range of *P. averano* (Snow 1970). Wallace's sight record near Belém (Pará) is puzzling, since it is so far outside the normal range, and is also omitted. Without doubt the species occurs more widely in the south of Guyana and Surinam than is shown. For French Guiana there appear to be no more exact records than the general locality 'Cayenne', used in the older literature, and a single symbol is placed in a likely locality in the centre of the country.

P. nudicollis. The great majority of the published Brazilian records are plotted (Hellmayr 1929, Pinto 1944), and all those published for Paraguay and Argentina (same authors, Laubmann 1940). Additional Brazilian records are based on specimens in the museums of Belém, Rio de Janeiro, São Paulo, New York, Washington, Philadelphia and Leiden. Not all records are shown for the area where records are concentrated in the southeastern Brazilian coastal region.

The distribution of *P. nudicollis* at its northern limit is poorly known. The most northerly record but one was collected in the vicinity of Bahia (by R. H. Beck, specimen in New York), but the exact locality is not known.

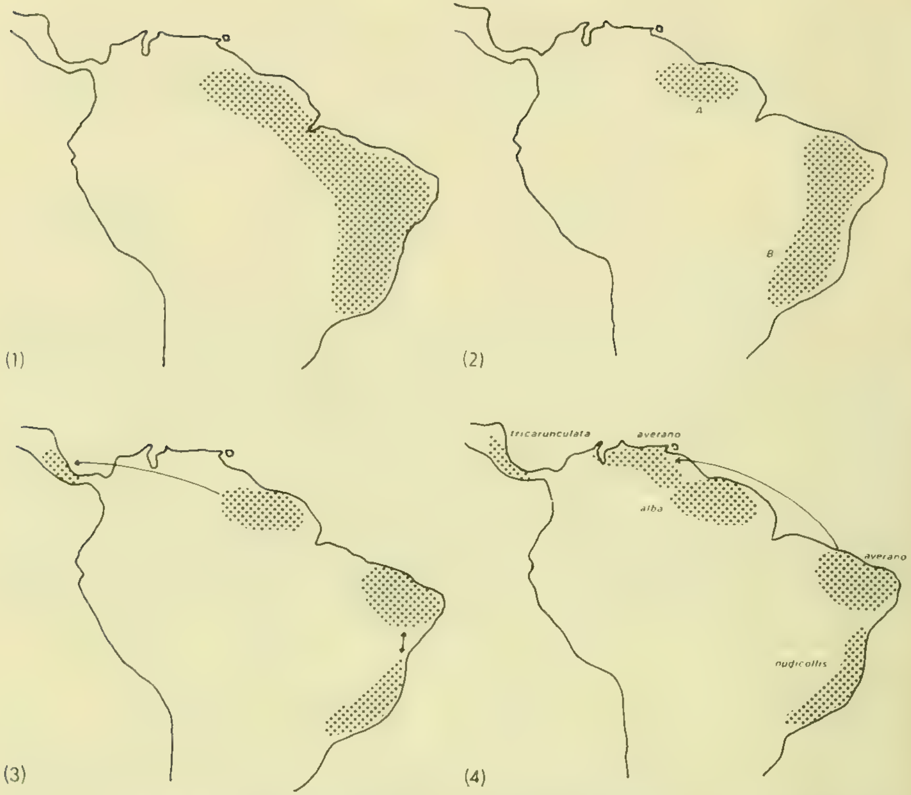

Fig. 4. Hypothetical distributional history of the genus *Procnias.* (1) Ancestral form in some part of northeastern South America. (2) First split, leading to one population in the Guiana highlands and the other in the eastern Brazilian highlands. Subsequent differentiation of adult males: A, wattles concentrated round beak, few in number; throat feathered; B, wattles concentrated on throat; throat otherwise bare. (3) Later splits, probably by long-range colonization of Central America by the western population, leading to differentiation of the four presently existing species. (4) Long-range colonization of northern Venezuela by *P. averano.*

DISTRIBUTION IN RELATION TO FOOD TREES

It is probable that the size, and especially the gape size, of bellbirds has evolved in close relation to the size of the fruits on which they feed, and that their generally montane distribution is similarly related to their food trees. It is not possible to do more than suggest these connections and back up the suggestion with fragmentary evidence, until more complete data are available on the tree families on whose fruit bellbirds mainly feed. The importance for specialized neotropical frugivorous birds of three plant families (Lauraceae, Burseraceae and Palmae) has been discussed in an earlier paper (Snow 1971). The first two of these families are important in the diet of *P. averano* in Trinidad (Snow 1970) ; in particular, the young are fed largely on lauraceous fruits, and the breeding season coincides with the time when most species of Lauraceae are in fruit. Palm fruits, on the other hand, are mostly too large or too firmly attached for bellbirds to be able to take them (they are important in the diet of some of the very large cotingas usually known as fruit-crows). There is no detailed information on the diet of the other bellbirds, but Skutch (1969) mentions the importance of the Lauraceae in the diet of *P. tricarunculata*.*

It is unfortunately the case that the Lauraceae and Burseraceae are taxonomically difficult families. The Lauraceae, in particular, contains very many species with relatively slight morphological differences between them. This may, in fact, be a direct consequence of interspecific competition between them for dispersal by birds, which would be expected to result in differences in fruiting seasons (Snow 1965) and perhaps other ecological characters, while the fruit characters would be held within acceptable limits of size, shape and nutritional quality.

Like other cotingas, bellbirds swallow fruits whole. The fruits must therefore be able to pass between the rami of the lower jaw, which are bowed markedly outwards, doubtless as an adaptation for swallowing fruits of large size. It is this outward bowing of the rami of the jaw, combined with the rather low crown, that gives the bellbirds their frog-like appearance, already mentioned. The maximum size of the fruits which they can swallow can thus be assessed directly from the skull, if some allowance is made for the thickness of the tissues overlying the bone. (A similar measurement for manakins of the genera *Manacus* and *Pipra* gave figures which agreed very closely with the upper limit of size of fruits seen to be taken in the field.)

The single available skull of *Procnias*, an unsexed but almost certainly adult male *P. nudicollis*, can 'swallow' fruits of diameters up to 22 mm. The width of the gape measured externally on study skins of this species is 24–26 mm in males and 21–23 mm in females. On the same basis, and assuming that the measured skull is of average size, measurements for all four species give the following maximum diameters of exploitable fruits :

	males	females
P. alba	24–27	20–21
P. averano	22–24	19–22
P. nudicollis	21–23	18–20
P. tricarunculata	21–23	19

Table 2 shows that the four species of bellbirds are each able to eat almost all the known species of lauraceous fruits in their respective habitats. In French Guiana, for instance, only one species of the Lauraceae has fruits much too large for *P. alba*, and this is the well-known Greenheart *Ocotea rodiaei*, whose fruits have a woody pericarp and are obviously adapted for dispersal in quite a different way. Again, all but one of the known Panamanian species for which Allen (1948) gives measurements are within the range that can be taken by *P. tricarunculata*, and their upper limit is exactly the bellbird's upper limit.

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* Pelzeln (1868) most surprisingly recorded snails in one of three stomachs of *P. nudicollis* examined the other two contained only fruit remains; and Burmeister (1856) gave the food of this species as fleshy fruits, with insects an additional item ('wohl nur als Zukost' – merely as seasoning). In view of the more recent evidence for an exclusively fruit diet these early records might seem questionable; yet the extinct frugivorous pigeon of Mauritius, *Alectroenas nitidissima*, was said to eat molluscs as well as fruit (Goodwin, 1970), and other mainly frugivorous pigeons certainly do so. Possibly the low calcium content of a pure fruit diet requires an occasional supplement from other sources, perhaps especially for egg-laying females.

TABLE 2

Diameters of fruits of the Lauraceae from Panama, Trinidad, French Guiana and S.E. Brazil and maximum size of fruits that can be swallowed by the four species of *Procnias* occurring in these areas

Area		Panama	Trinidad	French Guiana	S.E. Brazil
Procnias sp.		*tricarunculata*	*averano*	*alba*	*nudicollis*
Maximum diameter of exploitable fruit		♂ 21–23 ♀ 19	♂ 22–24 ♀ 19–22	♂ 24–27 ♀ 20–21	♂ 21–23 ♀ 18–20
Number of species of Lauraceae with fruits of diameter (mm)	30 +	–	–	1	–
	27	1	–	–	–
	25	–	–	–	–
	23	–	1	–	–
	22	1	1	–	–
	20	3	–	1	1
	19	–	1	–	2
	18	2	1	1	2
	17	1	–	2	–
	16	1	–	–	–
	15	3	1	4	5
	14	–	–	3	1
	13	1	5	2	2
	12	1	4	5	3
	11	3	3	5	2
	10	6	4	2	8
	9	2	1	1	2
	8	4	1	6	6
	7	2	–	4	3
	6	2	–	5	7
	5	1	–	–	4

Notes. Botanical data for Panama from Allen (1948); for Trinidad from Marshall (1938) and personal measurements; for French Guiana from Lemée (1952–6); and for S.E. Brazil (States of Rio de Janeiro and São Paulo) from Mez (1889).

Many species of Lauraceae are found at all altitudes in neotropical forests, but there is little doubt that they are numerically more important in montane than lowland forest. For Trinidad, the lists of trees per 100 acres in different forest types given by Beard (1946) show that in six faciations of lowland forest ('Evergreen Seasonal Forest') there are 4–6 species of Lauraceae in totals of 87–104 tree species; while in Lower Montane Rain Forest, which grows at c. 250–800 m above sea level, there are 10 species of Lauraceae in a total of 87 tree species. A recent monograph on the lauraceous genus *Persea* (Kopp 1966) shows that in Central America, where this genus is strongly represented, the majority of the species have been recorded between 1000 and 2000 m above sea level, and rather few below 1000 m. Skutch

(1969) draws attention to the confusing variety of species of Lauraceae in the montane forests of Costa Rica. By contrast, only two species of *Persea* are recorded by Kopp from the whole of the vast lowland Brazilian State of Amazonas.

To what extent the bellbirds' breeding seasons in areas other than Trinidad, and their seasonal movements, especially the vertical migrations in Central America and eastern Brazil, are related to the fruiting seasons of their food trees must await future investigation. The evidence available so far suggests that the trees of a few families will be found to play a key part in their annual cycle, just as they seem to have in determining their distribution and morphology.

ANNUAL CYCLE

No nest has been found of any bellbird except *P. averano* in Trinidad (Snow 1970). In spite of this, it is fairly certain that the two species which breed at the highest latitudes, *P. tricarunculata* in the north (about 9 to 14 degrees north) and *P. nudicollis* in the south (about 12 to 26 degrees south), follow the spring/summer breeding regimes that are prevalent in Central America and eastern Brazil (Skutch 1969, Euler 1867). The available moult data are difficult to evaluate, but it seems that adults begin to moult during the breeding season or immediately after it, while young birds begin a complete moult shortly before the breeding season begins. The information on which this conclusion is based is discussed more fully in a forthcoming survey of moult cycles in the family Cotingidae.

P. alba and *P. averano*, living mainly within 10 degrees of the Equator, certainly have less clearly defined seasons of breeding and moult over most of their ranges than the other two species. *P. averano* in the centre of the Northern Range of Trinidad, at the northern limit of the species' range, has a main egg-laying season in April–July and a minor season in October–November. Adults begin to moult between April and August, and young males on average considerably earlier, in March and April. The moult records for *P. alba* show no clear seasonal pattern.

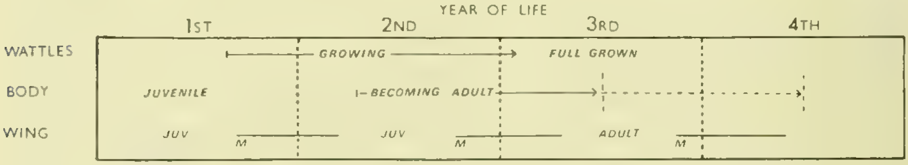
After breeding, *P. tricarunculata* in Costa Rica moves down from the highland forests to the lowlands. Thus at an intermediate level Skutch (1969) records them as present chiefly in July–September and January–March, and they are recorded in the lowlands mainly in winter. Similarly *P. nudicollis* moves down to lower altitudes in the southern winter, but little seems to have been recorded in detail. All four species undertake local movements which may or may not be seasonal, apparently in connection with the fruiting of their food trees.

PLUMAGE SEQUENCES

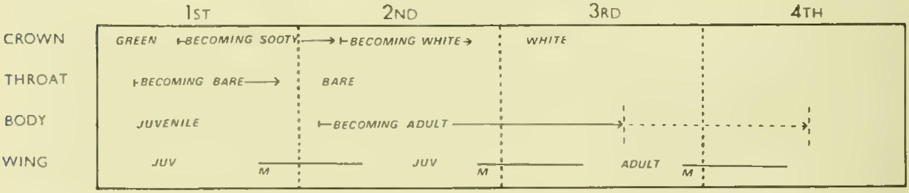
Male bellbirds take a long time to acquire fully adult plumage, and in the course of acquiring it pass through a succession of individually highly variable plumage stages. The moulting process is probably slow, and it is often found that the colour of the newly acquired flight or tail feathers changes progressively along the row, showing progressively more adult characters. Often too the base of a feather is markedly more adult in colour than the tip. Much of the variability appears to result from a variation in the relative timing of the moults and the changes in the bird's hormonal state. Another source of variability is the haphazard replacement of wing-feathers, especially secondaries, out of the normal sequence. Furthermore, it is not uncommon for the wing moult to be arrested before it is complete. It is not possible to tell from a study of skins whether, after being arrested, moult is resumed from the point where it stopped, but it is certain that a moult sometimes begins, or is resumed, at some intermediate point in the normal sequence. Feathers or parts of feathers that are transitional between juvenile and adult type, especially those transitional to white, tend to show a 'peppered' effect, being finely spotted with the remnants of the dark colour that is being lost.

Because of their more synchronized annual cycle, it is much easier to work out the time of the plumage changes in *P. tricarunculata* and *P. nudicollis* than in the other two species. For the purpose of working out the changes from juvenile to adult male plumage, it is assumed that all *P. tricarunculata* were hatched in June and all *P. nudicollis* in December (see previous section). It is unlikely that this assumption will introduce an error of more than two months in ageing a specimen.

Assuming these hatching dates, the evidence from dated specimens shows that the sequence and timing of plumage change are very similar in these two species (Figure 5). Young males undergo a succession of complete annual moults, beginning when


YEAR OF LIFE
1ST
2ND
3RD
4TH
WATTLES
BODY
WING
GROWING
FULL GROWN
JUVENILE
BECOMING ADULT
JUV
M
JUV
M
ADULT
M

P. TRICARUNCULATA


1ST
2ND
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4TH
CROWN
THROAT
BODY
WING
GREEN
BECOMING SOOTY
BECOMING WHITE
WHITE
BECOMING BARE
BARE
JUVENILE
BECOMING ADULT
JUV
M
JUV
M
ADULT
M

P. NUDICOLLIS

FIG. 5. Generalized time-table of acquisition of adult plumage by males of *Procnias tricarunculata* and *P. nudicollis*. Body plumage: the broken line represents the period within which fully adult plumage is acquired (individually variable). Wing: the lines labelled M indicate periods of moult of the flight-feathers.

they are a little under a year old. At the first complete moult the wing and tail are replaced again by juvenile feathers; the head and body feathers are replaced, variably and perhaps more gradually than the wing and tail, by feathers of more adult type. In some birds, the last wing and tail feathers to be replaced also show a tendency towards adult colouration. When the bird is a little under two years old another complete moult leads to the assumption of wing and tail feathers of adult or nearly adult type, and the head and body also become nearly adult in colour. In some individuals completely adult body plumage is acquired without a further wing moult, presumably by gradual replacement ; in others, the fully adult plumage is not acquired until after the third complete moult. The replacement of odd wing and tail feathers between these complete moults may result in irregularities, with a few feathers of more adult type than the rest.

In *P. tricarunculata*, the wattles begin to grow when the male is between six months and a year old (assuming hatching in June), and they evidently grow fast, those at the gape much faster than the central one, since by the end of the first year they may be up to 20 mm long. They do not then grow much more during the following year. In *P. nudicollis* the male's throat becomes bare in the course of the first year.

It is difficult to investigate the body moults which do not involve a colour change, but there is probably a complete body moult in the first few months of life. In *P. nudicollis* the crown becomes sooty-black in this period, to be replaced by white in the first months of the second year.

In *P. averano* and *P. alba* the less well-synchronized annual cycle (which may also differ in different parts of the species' ranges, according to the regime of wet and dry seasons) and more frequent irregularities of moult sequence make a reconstruction of plumage changes more difficult ; but the observed changes in plumage in a male *P. averano* in Trinidad, of known age (Snow 1970), provide a useful time-scale for part of the juvenile period. It seems that the plumage sequence and timing are very much the same as in *P. tricarunculata* and *P. nudicollis*. There is a succession of full moults, apparently starting when the bird is nearly a year old. After the first, the wing and tail are still of juvenile type, after the second they are sub-adult, and after the third fully adult in colour. In *P. averano* an early moult, probably of the whole head and body, leads to the assumption of a sooty crown, and this is replaced by the brown crown of the adult during the second year. After the first full moult the back also becomes sooty in colour rather than green, and later often grey-brown, before the very pale grey adult colour is acquired. The change is variable and probably depends on the relative timing of hormonal changes and of moults.

In *P. averano* the pale juvenile throat feathers are replaced by sooty feathers at about the same time as the sooty crown is acquired. The wattles probably develop at the age of about a year ; in the Trinidad juvenile they were just visible, in the field, at the age of 16 months. In the only specimen of *P. alba* examined at the appropriate stage, the wattle was present but short when the bird was half-way through its first wing moult, presumably at an age of just over a year.

THE WATTLES

The age at which the wattles first appear has just been mentioned. In all three of the species with wattles, they begin to grow in the young male while the plumage is still wholly juvenile, and are a good size, though probably not full-grown, by the time that the adult plumage is complete. The wattles are bare, shiny and blackish in *P. tricarunculata* and *P. averano*; in *P. alba* the single wattle is black and is sparsely covered with small white star-like feathers. The bare skin of the throat of *P. nudicollis* is greenish; it is not completely bare, but is sparsely covered with black bristles. Similar bristles grow between the wattles on the throat of *P. averano.*

The histological structure of the wattles has not been investigated. Schomburgk (1848) asserted that the wattle of *P. alba* is hollow and muscular, and in direct communication with the palate, and that it can be inflated at will. Waterton (1824) had earlier said much the same thing. As a result the older illustrations of *P. alba* usually show it with the wattle standing straight up like a unicorn's horn. From close observation of a captive bird, Quelch (1892) refuted Schomburgk's assertion, describing the wattle as made up of fine elastic tissue. Little can be added so far as the histology goes, except that the wattle must also contain muscle fibres, as Salvin (1865) suggested for *P. tricarunculata.*

The first good account of the wattles in life was given by Quelch. Writing of a male *P. alba* in captivity in British Guiana (Guyana), he wrote: 'When the bird is about to utter its characteristic notes, this appendage slowly becomes greatly elongated – to as much as five inches, I have observed at times. At the conclusion of the note, the organ may remain extended till the next note, or it may be partially retracted; but when a long interval takes place, the structure is always allowed to shrink up to about half an inch or an inch in length, at will; and it then hangs against the beak.' Similarly Snow (1961) observed that when a male *P. alba*, observed in the wild, had finished a bout of calling the wattle contracted to about a third of its former length before the bird flew off to feed. Crandall (1948) also reported that in a captive *P. tricarunculata* the wattles enlarged to about three times their usual dimensions when the bird was calling.

The mass of wattles on the throat of *P. averano* does not alter so noticeably when it is calling; but they are made more conspicuous by the erection of the feathers of the upper breast, which push the bird's black 'beard' forwards (Snow 1970). It is probable, however, that in this species too the wattles can be extended by muscular action. Thus W. G. Conway (*in litt.*) noted that in a captive *P. averano* in the Bronx Zoo, New York, the wattles appeared shrivelled up when it stopped calling and began to moult.

It seems clear that the display of the wattles, in all three species, is closely connected with calling, and there is no doubt that the main function of all the male's displays is to attract females to the calling perch, on which mating takes place (Snow 1970). Presumably the wattles, in combination with the striking plumage and associated behaviour, play an important part when the female is at close quarters; certainly in *P. averano* the male's performance appears to rivet the female's attention. Crandall (*loc. cit.*) reported that a female *P. tricarunculata* in captivity appeared to be attracted by the dangling wattles of a male and at least once reached forwards as if to peck at them. This is almost certainly not normal behaviour, since in *P. averano*, and probably also in *P. alba* (Snow, in press), the male and female stay two or three feet apart during courtship, until the male leaps, with an explosive call, onto the female. Nevertheless, the wattles may perhaps be regarded as structures analogous to the dangling silky fringes of the modified secondary feathers of the Cock of the Rock *Rupicola rupicola*, which attracted a courting female to lean forward and nibble at them (Snow 1971).

The evolution of extensible wattles as a result of sexual selection has brought with it a concomitant disadvantage, though probably not a serious one, for the males of the two species whose wattles grow from the base of the beak. Crandall mentioned that the long wattles of a captive *P. tricarunculata* were a positive nuisance to the bird when it wanted to feed ; and Snow (1961) noted that a male *P. alba*, when calling, had to ensure that its wattle was hanging down on the right side before it could begin one of its calls, which involved swinging the head to the left.

VOICE

Male bellbirds utter what are perhaps the loudest of all bird calls ; the females and nestlings, at least of *P. averano*, are almost or completely silent (Snow 1970). The main characteristics of the calls of the four species are described and illustrated in the following sections, which are followed by a brief discussion of functional, mechanical and evolutionary aspects of the calls.

Procnias averano

Males of the Venezuelan population have three distinct calls : a single, very loud *bock* (Plate 1(A)) ; a repeated, less loud *tock, tock, tock* . . . (Plate 1(B)) ; and a more musical, double *kay-kong, kay-kong*, . . ., repeated more slowly than the *tock, tock, tock* (Plate 1(C)). The single *bock* is remarkable for the rather even distribution of energy over a wide frequency range, with the emphasis on the second harmonic, and for the very sudden beginning of the note. These features combine to give the note its sudden, unmusical hammer-like quality. The repeated *tocks* are very similar in form to the *bock*, but only two instead of six harmonics above the fundamental are apparent in the sonogram.

The double *kay-kong* is of more complex form : the main part of the first syllable is very similar in form to the *tock* but more drawn out, while the second syllable has almost all its energy concentrated at the fundamental frequency, thus producing a more musical and lower-pitched note. In the first syllable, the harmonics begin a little after the fundamental frequency is sounded. Both syllables begin with a preliminary pulse of energy whose upper frequency is intermediate between the frequency of the second and third harmonics. Exactly the same preliminary pulse is apparent at the beginning of the *tock*, where it is less distinct in time from the main part of the note, while in the *bock* it is, as it were, attached to the main part of the note, so that there is a sudden descent in pitch which is most marked in the higher harmonics.

The *bock* of the Trinidad bird (Plate 1(D)) is even more remarkable for the even distribution of energy over a wide frequency range, and for its short duration, which gives it an even duller, more hammer-like quality than the *bock* of the Venezuelan bird. The repeated *tocks* (Plate 1(E)) are simply less loud versions of the *bock*. The refinements of the beginning of the call, noted for the Venezuelan bird, are not present.

Males of the Trinidad population now use only these two calls, the *bock* and the repeated *tock*, but, as Snow (1970) has pointed out, there is good evidence that a third call was being used by the Trinidad population in 1893, when Brewster and Chapman visited the island (Brewster & Chapman 1895). This third call was disyllabic and may have been similar to the *kay-kong* of the Venezuelan population (but see footnote to p. 388). The implications of this loss of part of the repertoire are discussed in a later section.

Snethlage (1928) has given the only account of the calls of the population of *P. averano* in northeastern Brazil. He wrote : 'Zwar verfügt er nur über zwei Töne : einen schweren und einen leichteren Schlag, die den Hammerschlägen auf Eisen gleichen. Ein schwerer Schlag, kleine Pause, dann regelmässige leichte, das ist der Gesang, der zur Zeit der ersten Regen (im August–September) weithin zu vernehmen ist.' (They use only two notes : a loud and a softer note, which sound like the blows of a hammer on iron. A loud blow, a short pause, and then regularly repeated and less loud notes – that is the song, which is to be heard from afar at the beginning of the rains (August–September).)

Before uttering the explosive *bock* the bird opens its beak very wide, and the call is given when the beak is fully open (Snow 1970). Brewster & Chapman described the calling bird as throwing its head forward and downwards with a violent, convulsive jerk, but this is certainly not normal behaviour. When the repeated *tocks* are being uttered the beak remains open, the lower mandible merely moving down and then upward again with each note.

Procnias nudicollis

Two calls are uttered : a single *bock* (Plate 2(A)) and a repeated call (Plate 2(B)). The *bock* is extremely similar to that of *P. averano* ; the repeated call is probably homologous with the repeated *tock* of *P. averano*, but it is of most peculiar structure : a less loud but otherwise apparently identical version of the *bock* is followed, about 0·08 second later, by a very loud and pure high-pitched note, exactly an octave above the fundamental frequency of the first note. The two very different and partly overlapping notes give the impression of a hammer striking an anvil a glancing blow so that it rings.

Greenewalt (1968) presented an oscillogram (time-amplitude diagram) of this call, together with a time-frequency plot, giving it as an example of a call in which two independent sound sources must be involved. This aspect of the call is discussed more fully in a later section (p. 387).

When preparing to utter the explosive *bock*, the bird is described as opening its mouth very wide, perhaps inhaling ; it then bows forward as the *bock* is uttered. The continuing, repeated notes are accompanied by coordinated nodding or slight bowing (manuscript notes by R. Ward, who made the recordings used for the sonograms).

Procnias alba

Of the four bellbirds, this species has by far the most musical voice, and is the one which gives the genus its popular name. There are two calls : a double *kong-kay*

(Plate 2(C)) and a long drawn-out *do-i-i-i-ing* (Plate 2(D)). This second note, attenuated to a silvery chime as it filters down through the forest trees, is among the most beautiful sounds of the Guiana forests.

The two notes of the *kong-kay* are similar in structure, but the second is a little higher pitched than the first (fundamental frequencies of about 1·8 and 1·7 kHz respectively). Though it is difficult to be certain of this, it seems from detailed inspection of the sonograms that the two overlap in time, and thus are presumably produced by two independent sound sources.

The utterance of the double *kong-kay* is sometimes accompanied by a characteristic movement (Snow 1961). The bird turns sharply to the right to utter the first syllable ; then with beak still wide open it rotates the body rapidly through an arc of about 100 degrees, to make the second note facing to the left. The wattle normally hangs down to the right of the beak, so that it flies out horizontally as the bird swings to the left. If it happens to be hanging down on the left side, the bird manœuvres it to the right side before calling.

The drawn-out *do-i-i-i-ing* is a pure note of very even pitch, with a single harmonic. It is usually more or less clearly broken into two notes (Plate 2(D)), the second syllable being shorter and dying away with a slight tremolo. Because it tends to be disyllabic, it has been written as *do-rong* (Quelch 1892, Snow 1961).

Quelch's detailed description of the calling of a captive male of *P. alba* in Guyana is worth quoting in full, since the way in which the air is inhaled and the movements associated with the calls are relevant to the problem of the two sound sources, discussed in a later section (p. 387). 'When the appendage is fully elongated [see earlier, p. 382, for distension of the wattle], the bird suddenly inflates its lungs, right and left, by inhaling – almost by a swallowing action – two great draughts of air ; but the method by which this is done depends upon which of its two characteristic notes it intends to utter. When the notes "Kong-Kay" are uttered, the action of inflation has been performed by two distinct inhalations of air, one with the head turned to the right and the other immediately after to the left. At the moment of utterance of the notes, the head is turned to the right for the "Kong", and then suddenly – so suddenly that it almost startles the observer – the head is swung round to the left for the "Kay", which is issued with a strikingly loud, piercing and metallic ring or clang – so loud and shrill indeed that, if the observer is close by, the ears are actually deafened for the moment by the sharpness of the sound.

'When, however, the sweet, musical, and deeply-toned bell-like notes "Do-rong" are about to be uttered, the bird is observed simply to hold its head forward, and to make two distinct gulps of air ; and then, holding its beak upwards and slightly extending its neck, the notes are rolled out, as it were, with full voice and roundness and resonance.'

Procnias tricarunculata

Of the four bellbirds, this species has the least highly developed repertoire. Skutch (1969) has given the fullest account of its voice. There are apparently only two distinct notes, one 'loud and strong but dull and throaty' (*buck*), the other much sharper and higher in pitch (*wheat*). The sonograms show less difference between these two notes than might be expected from Skutch's description (Plate 2(E)), but they are in fact quite distinct. The *buck* has much of its energy centred, rather diffusely, round frequencies of about 1·75 and 3·5 kHz, with some energy at very low frequencies. This frequency distribution presumably accounts for the dullness of the tone, which Skutch likens to a wooden clapper, while the roughness of the sound probably comes from the irregular pattern of frequencies at the beginning of the note. The *wheat*, on the other hand, has its main frequency band about 0·3 kHz higher than that of the *buck*, has no very low frequencies and shows an orderly series of diminishing harmonics.*

It is clear from Skutch's account that, although the two notes are commonly uttered in succession, to form the phrase *buck wheat*, they are also given in every possible combination. The significance of this lack of organization in calling behaviour is discussed in a later section (p. 388).

FUNCTION OF THE CALLS

The epigamic function of these very loud calls has already been briefly mentioned (p. 369). There is no doubt that they are advertising calls, and one of the means by which males attract females to their display perches. Why such a very loud call should have evolved in this genus is not clear ; but it should be noted that many forest birds, in which the males display at traditional sites, have loud advertising calls. In the Cotingidae very loud calls, though of a different kind from those of the bellbirds, are uttered by males of other large species, in the genera *Tijuca*, *Perissocephalus*, *Pyroderus*, *Cephalopterus* and *Lipaugus*. Males of other genera are less noisy, but these advertise themselves from a distance by making themselves visually conspicuous. The bellbirds are peculiar in having two extremely effective methods of making themselves conspicuous from a distance. A mainly white bird calling very loudly from an exposed tree-top - a usual calling perch - could hardly advertise itself more effectively. At least in *Procnias averano*, the later stages of courtship display are carried out beneath the canopy of the forest, on comparatively low perches, and are silent except for the loud *bock* which accompanies the mating leap.

One of the ways in which vertebrates can locate sounds is by comparison of the time of arrival of the sound at the two ears. This is possible only if the sound begins or ceases abruptly (Marler 1955). The extraordinarily sharp beginnings of the bellbirds' calls should therefore make them especially effective in this respect, and in fact a bellbird calling at a distance can be accurately located by the human ear, as long as one is in the open. It is, however, rather difficult to locate a calling bellbird if one is under the forest canopy, probably because the sound is reflected with varying degrees of strength from the trees all round.

MECHANISM

The vocal mechanism which enables bellbirds to produce explosively loud calls of varied structure and complexity has not been fully elucidated. Greenewalt

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* In an earlier account Ridgway (1905) described the call as 'like a heavy stroke with a hard mallet on a hollow log of hard wood followed immediately by a wonderfully loud, clear and prolonged whistle'. This is endorsed by Slud (1964) ; but the only available recording matches Skutch's description closely, since the *wheat* is not prolonged. Perhaps there is local or even individual variation in the calls of this species

(1968) has discussed the physical basis of sound production by the avian syrinx and gives the reasons for believing that the sounds produced depend on the vibration of syringeal membranes alone, and that little or no importance is attributable to the resonance of the trachea, or to modulation of the sounds in the larynx. Greenewalt concluded from the anatomical evidence, and from early experimental evidence, that the only membranes actively involved in sound production were the two internal tympaniform membranes. Thorpe & White (1969), however, have pointed out that the external tympaniform membranes are also involved, at least in some species.

It has been known for a very long time (Herissant 1753) that the production of sound by the syrinx depends on air pressure in the interclavicular air sacs which surround the syrinx, and Rüppell (1933) confirmed this with experiments on an isolated syrinx. Greenewalt took the theoretical analysis much further, and showed that 'high amplitude, for phrases rich in harmonic content, must be associated with *increased pressure in the clavicular sac*'. Since the calls of bellbirds are both rich in harmonics and extremely loud, it seems certain that they must build up an unusually high air pressure in their interclavicular air sacs. Discussing the relationship between pulse length and harmonic content, Greenewalt further pointed out that 'the more nearly one approaches a simple pulse the more terms one will find in the harmonic spectrum. The extreme case (a sharp pulse of very short duration) will produce a harmonic spectrum containing an infinite number of terms at constant amplitudes.' The single very loud calls of bellbirds perhaps illustrate this principle more clearly than any other bird calls.

Both *P. alba* and *P. nudicollis* utter calls in which two separate sound sources appear to be involved. The existence of two separate sound sources in birds' calls has been dealt with at length by Greenewalt, who considered that the right and left internal tympaniform membranes are responsible, acting independently under the influences of their separate musculature and innervation. This interpretation has been questioned by Thorpe & White (*loc. cit.*). The description of the calls of the four bellbird species, given above, can add nothing to this highly technical controversy. The behaviour associated with the double call of *P. alba* does, however, suggest the possibility that the production of sound by two vibrating membranes may be linked with the exhalation of air from the two bronchi successively. In the literature on the working of the avian syrinx there appears not to have been any serious suggestion of independent operation of the two lungs and bronchi ; but this would seem to be mechanically more efficient than their obligatory simultaneous operation in the case of sound produced independently by the two internal tympaniform membranes, since the flow of air from the right bronchus, for instance, would be largely wasted if the left membrane alone were being activated. Quelch did not suggest it, but his account of the calling of *P. alba*, quoted above, suggests the possibility that the turning of the head to right and left might be linked with the asymmetrical functioning of the bronchi and lungs.

EVOLUTION OF THE CALLS

The characteristics of the calls which suggest the phylogenetic division of *Procnias* into two pairs of species have been briefly mentioned on pp. 371–372. *P. averano* and *P. nudicollis* both have a single very loud monosyllabic call, the *bock*, of very similar structure in each. Both also utter a less loud, regularly repeated call, in structure very similar to the *bock*, except that in *P. nudicollis* there is a second, high-pitched element in the call, which is missing in *P. averano*. Both *P. alba* and *P. tricarunculata* utter a disyllabic call, of which the second note is higher-pitched than the first, but there the resemblance ends ; the two parts of the call of *P. tricarunculata* are not so closely coordinated as they are in *P. alba*, and the quality of the calls differs in the two species.

Snow (1970) described how a male *P. averano* in Trinidad, colour-ringed as a nestling, had still not perfected its call when it was over two years old. It seems probable that a slow learning process is involved in the achievement of the fully adult call by young birds, and it may well be that the presence of calling adults is necessary. If this is so, some elements of the full vocal repertoire might well be lost in a very small, isolated population if for some reasons the numbers sank very low and included few or no old males. Snow (*loc. cit.*) suggested that this may account for the loss, in the Trinidad population of *P. averano*, of an element present in the vocal repertoire of the Venezuelan birds.* In the case of long-distance dispersal, leading to the establishment of a new isolated population, this is even more likely to be accompanied by a reduction of the vocal repertoire, since dispersal most commonly involves young birds. This could account for the lack of differentiation in the calls of *P. tricarunculata*, which on quite different grounds seems likely to have arisen as a result of long-distance dispersal from some area far to the east, perhaps the Guiana highlands (Figure 4). The throaty quality of the *buck*, and the varied sequence of *buck* and *wheat* described by Skutch, are rather reminiscent of the harsh and irregular calls of young males of *P. averano*. Subsequent observations of *P. alba* in Guyana (Snow, in press) have shown that the calls of young males are very similar to those of *P. averano*. It may well be that in all four species the calls pass through very similar developmental stages before they are crystallized under the influence of the calls of fully adult birds.

SUMMARY

The genus *Procnias* is one of the many isolated and peculiar genera in the neotropical family Cotingidae. It represents the culmination of the tendency towards specialization for fruit-eating characteristic of the family, associated with marked sexual dimorphism and the emancipation of the male from the nest.

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* Brewster & Chapman's description (1895) of the voice of *P. averano* in Trinidad raises some interesting questions which will never be fully answered. In addition to the calls that are easily identifiable as the same as those given by Trinidad birds today, described by Snow (1970), these two authors describe a double *tui-ting*, which certainly suggests identity with the disyllabic call of the Venezuelan population (p. 383). There were, however, some clear differences in the Trinidad call, if Brewster & Chapman's description is to be relied on. 'Each *tui* is followed closely by a metallic *ting* which sounds exactly like an echo and appears to be of about the same duration and nearly as loud as the note it supplements. The *tui* notes are given so quickly that at first it did not seem possible for the bird to produce another note between them, and it was only after repeated observations we became convinced that the *ting* was an integral part of the *tui* call.' This is not the impression given by the distinctly disyllabic and well-spaced *kay-kong* of the Venezuelan bird (Plate 1(C)) ; indeed it seems much more like the repeated call of *P. nudicollis* (Plate 2(B)). One can only conclude that the vocal repertoire of isolated populations of bellbirds is labile, and that new elements may be gained as well as lost.

The four species, which are almost entirely allopatric, fall into two closely related pairs, *P. averano* and *P. nudicollis*, and *P. alba* and *P. tricarunculata*. Their present distribution suggests that the ancestral stock inhabited northeastern South America, that it first split into an eastern and a western form, and that each of these subsequently split into two species.

It is probable that the bellbirds' general body size, and especially the size of the gape, are related to the sizes of fruits of trees in the family Lauraceae, which provide a great part of their food.

The acquisition of fully adult plumage by the males takes about three years. In *P. averano* at least, the adult male's calls are not perfected until the third year of life. The mechanism by which the extremely loud calls are uttered is not fully understood, but there is evidence that two independent sound sources are involved.

There is some evidence that learning is important in the acquisition of the full vocal repertoire. The isolated Trinidad population of *P. averano* lacks one of the calls of the Venezuelan population. The lack of clear differentiation in the calls of *P. tricarunculata* may have resulted from a break in learning, consequent on the presumed long-range colonization of Central America by the ancestors of this species.

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PLATE 1

Sonograms of calls of *Procnias averano*.

A. Venezuela. The *bock*.
B. Venezuela. The repeated *tock*.
C. Venezuela. The repeated *kay-kong*.
D. Trinidad. The *bock*.
E. Trinidad. The repeated *tock*.

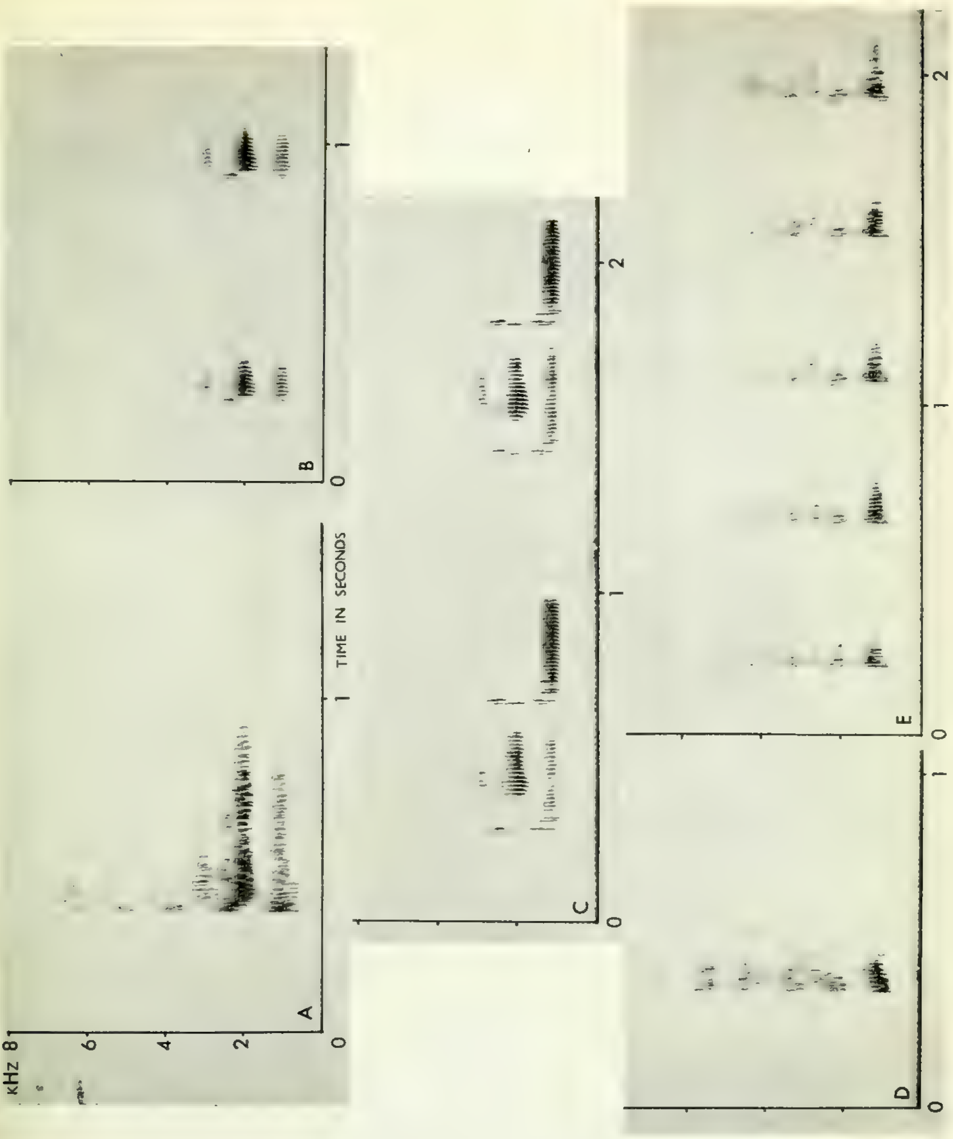
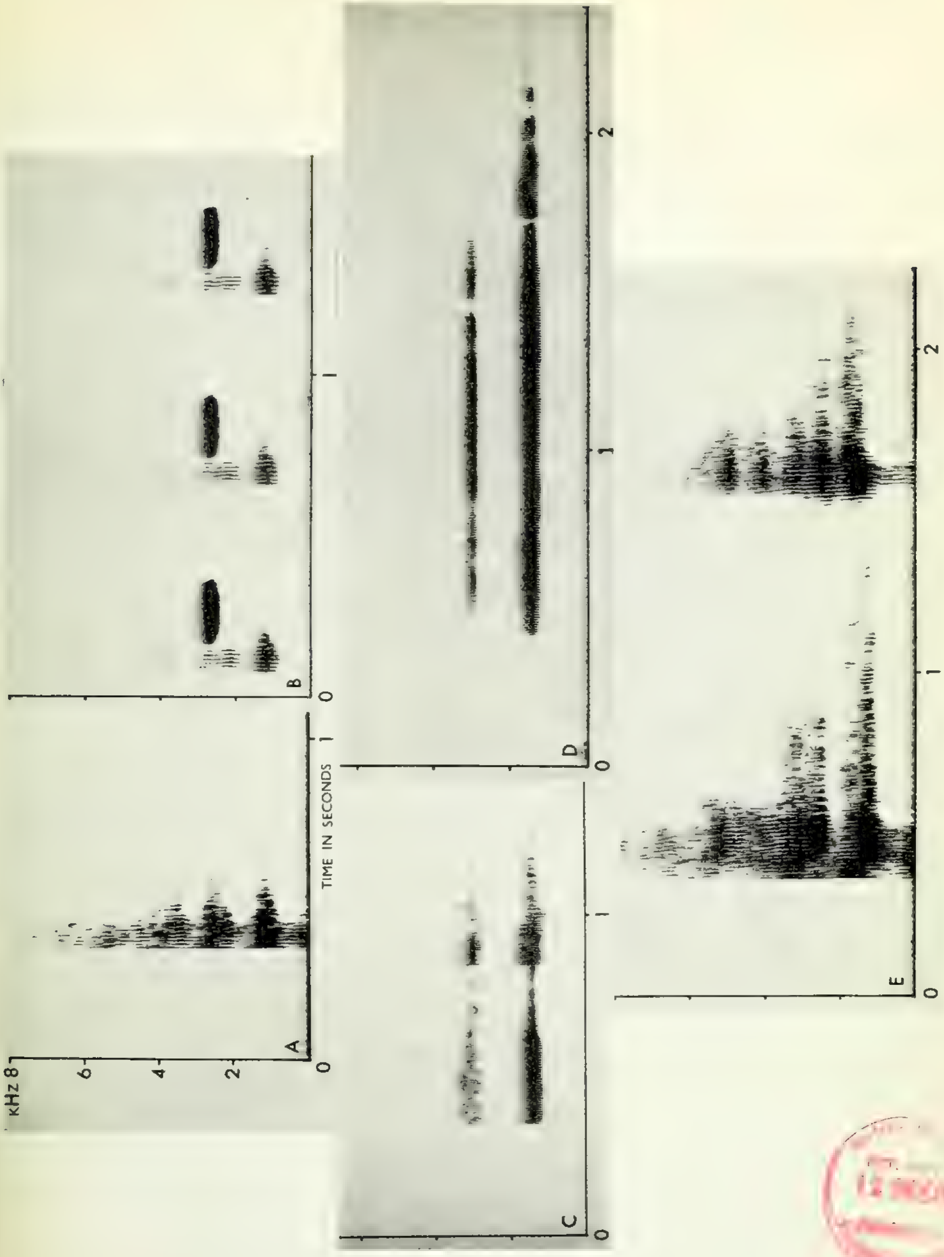

kHz 8
6
4
2
0
A
B
C
D
E
TIME IN SECONDS
0
1
2

PLATE 2

Sonograms of calls of *Procnias nudicollis*, *P. alba* and *P. tricarunculata*.

A. *P. nudicollis*. The *bock*.
B. *P. nudicollis*. The repeated call.
C. *P. alba*. The *kong-kay*.
D. *P. alba*. The *do-i-i-i-ing*.
E. *P. tricarunculata*. The *buck wheat*.


kHz 8
6
4
2
0
A
B
C
D
E
TIME IN SECONDS
0
1
2

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